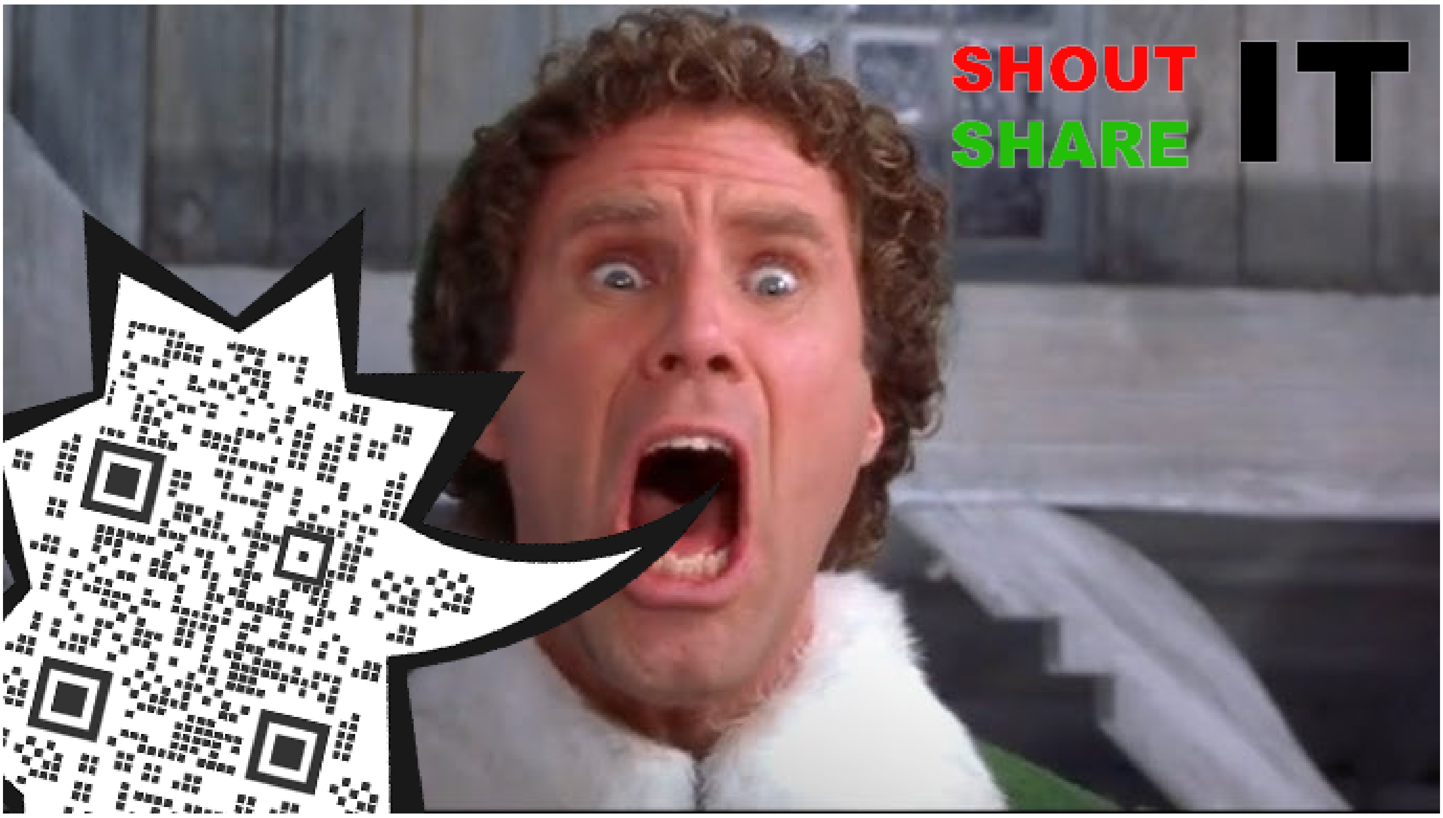
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The Great Basin Naturalist

VOLUME 37, 1977

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HE GREAT BASIN NATURALIST

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BREEDING BIOLOGY OF THE DOUBLE-CRESTED CORMORANT ON UTAH LAKE[1]

Ronald M. Mitchell[2]

ABSTRACT.— Research on the nesting of the Double-crested Cormorant (*Phalacrocorax auritus auritus*) was undertaken to determine the breeding biology of the bird on Utah Lake, Utah County, and the possible effects that diking Provo Bay would have on the cormorants breeding there. In 1973, two colonies in Provo Bay were visited weekly to determine laying dates, incubation period, clutch size, and hatching dates. Another colony, located on the dike of the Geneva Steel Works Reservoir near Orem, was visited daily during the spring and summer of 1973. At this colony egg-laying occurred from 13 April to 17 May. The average clutch size was 3.8, and the egg length and width averaged 60.50 mm x 39.05 mm. The average period of incubation was 28 days, and 29.5 percent of the eggs hatched, beginning on 20 May and ending on 9 June. The young weighed an average of 36 gm at hatching with a beak length of 17 mm and tarsometatarsal length of 11 mm. These measurements increased to 1543 gm, 73 mm, and 58 mm, respectively, in 23 days. The cormorant population on Utah Lake may be severely reduced by the proposed diking of Provo Bay.

There have been no detailed studies of the biology of the Double-crested Cormorant (*Phalacrocorax auritus auritus*) in Utah, other than a brief but noteworthy account by Behle (1958) of those birds that nested on Egg Island, Great Salt Lake. Two detailed studies of this subspecies have been conducted on the Atlantic coast (Lewis 1929, Mendall 1936), but no extensive accounts of breeding biology exist for Double-crested Cormorants found nesting inland. This lack of scientific data may be due in part to a lack of qualified and interested observers, but I feel it is principally due to the sentiment expressed in the following quotation:"God no doubt had his reasons for creating each living thing, but when he created the cormorant he did himself little credit" (Demille 1926). This attitude may account for the fact that the cormorant is likely the least understood water bird nesting in Utah.

Although there are three other subspecies (*P. a. albociliatus*, *P. a. floridanus*, *P. a. cincinatus*) found in North America, *P. a. auritus* is considered the most important due to its wide distribution, ranging from central Canada to Texas and from the Atlantic coast to Utah. The *P. a. auritus* populations in Utah are the westernmost breeding colonies found in the United States and provide excellent contrast for comparison with the previously studied birds nesting along the Atlantic coast.

The few published references that exist concerning Utah's cormorants are little more than sight records or brief mentions of nesting sites. Behle (1958) summarized the history of the seven cormorant colonies of which he was aware. At the time of his writing, all but two (Egg Island and Bear River) had been deserted or destroyed (Fig. 1). In addition I found a reference to an unreported colony located on White Rock, a small island located a few hundred yards northwest of Antelope Island, Great Salt Lake. A set of cormorant eggs was collected from there on 10 May 1901 (Woodbury et al. 1949). I also discovered an unreported colony located west of Bountiful in 1973.

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[1] This manuscript was prepared in partial fulfillment of the requirements for the degree of Master of Science in Zoology at Brigham Young University, Provo, Utah. The research was supported in part by a grant from the National Audubon Society.

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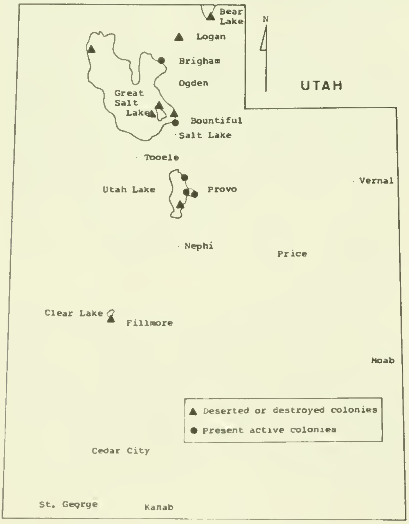
Behle (1958) did not mention Utah Lake as a nesting area, and it is mentioned only once in the other literature as a "former" nesting site (Woodbury et al. 1949). However, I was able to find unpublished references that included a record of four cormorant eggs collected in Provo Bay in 1920 (Bee 1920). Cottam (1927) stated that the Double-crested Cormorant nested on Utah Lake. In 1937 John Hutchings of Lehi (Bee 1937) reported that several sets of Double-crested Cormorant eggs were collected on Rock Island in Utah Lake (Fig. 2). James Bee (1946) found six active cormorant nests in a tree on the Geneva dike in May 1946 and stated that the birds had nested there for two or three years. Bee (1949) reported a trip to a large cormorant colony in Provo Bay, south of the Provo airport dike, that contained 150 pairs of nesting cormorants.

The purposes of this study were to obtain information on the breeding biology of the unreported colonies on Utah Lake, obtain data on the nesting ecology of inland nesting cormorants for comparison with the data already published concerning coastal nesting birds, determine the current status of Utah's cormorant population, and gather information to determine the impact on the nesting sites of the two colonies located in Provo Bay by the proposed plan of the Bureau of Reclamation to dike and drain the bay as part of the Central Utah Project.

The Study Area

There are three nesting colonies of Double-crested Cormorants located near Utah Lake. Two of the colonies are located in Provo Bay (Fig. 2), a shallow arm on the eastern side of Utah Lake. These have been designated the Springville and Bay colonies.


Bear Lake
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Salt Lake
Tooele
Utah Lake
Provo
Vernal
Nephi
Price
Clear Lake
Fillmore
Moab
▲ Deserted or destroyed colonies
● Present active colonies
Cedar City
St. George
Kanab

Fig. 1. Location of the deserted and active nesting colonies in Utah.

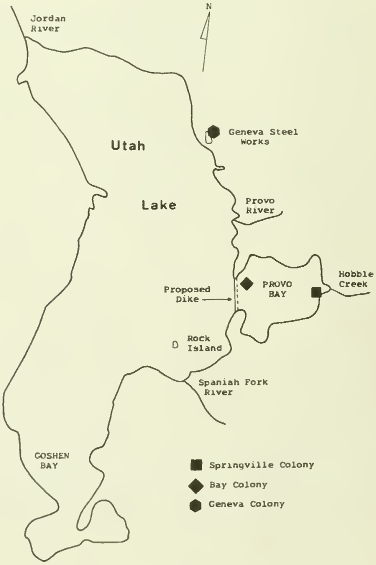
Jordan River
N
Utah
Lake
Geneva Steel Works
Provo River
Hobble Creek
Proposed Dike
PROVO BAY
Rock Island
Spanish Fork River
GOSHEN BAY
■ Springville Colony
◆ Bay Colony
● Geneva Colony

Fig. 2. Location of the three study sites on Utah Lake.

The water depth in this area varies from a few millimeters to 2 m and averages about 1 m. The principle vegetative types are hardstem bullrush (*Scirpus acutus*), tamarix (*Tamarix petandra*), cottonwood (*Populus fremonti*), and willow (*Salix amygdaloides*). The third colony is located 11 km north of Provo Bay at the United States Steel Company Geneva Works and is designated Geneva Colony (Fig. 2).

The Springville Colony is located 0.5 km due west of the mouth of Hobble Creek in a stand of cottonwood trees that range from 10–20 m in height and extend in a straight line west from the shore into the bay. The tree line, which is about 0.5 km long, was established in the late 1930's during low lake levels. The westernmost trees are dead, in 1 m of water, and in 1971 and 1972 the trees most distant from shore were used by cormorants for nesting. In 1973, apparently due to increased numbers, the birds moved eastward into some living cottonwoods that had previously been used exclusively by Great Blue Herons (*Ardea herodias*) for nesting.

The Bay Colony is located at the mouth of Provo Bay (Fig. 2), 2 km due south of the Provo airport. This site consists of a stand of cottonwoods and willows growing in an east-west line in about 0.6 m of water. In 1971 the area consisted of 18 trees ranging from 10–20 m in height. In 1973 cormorants nested with Great Blue Herons in one cottonwood and in four willow trees at the east end of the tree line.

The Geneva Colony is located on a diversion dike, built in 1940, that extends about 1.2 km within the reservoir. This artificial pond is located west of the steel plant proper and is about 0.2 km from Utah Lake. The water is contained by 3 m high earthen walls (Fig. 3). The water, which is over 6 m deep in most places, is used for cooling purposes in the steel-making process. The cormorants nested in one cottonwood and three Siberian elms (*Ulmus pumila*), all living, at the distal end of the dike. Great Blue Herons, Snowy Egrets (*Leucophoyx thula*), and Black-crowned Night Herons (*Nycticorax nycticorax*) nested in the same trees, while thousands of California Gulls (*Larus californicus*) nested on the dike itself.

METHODS AND PROCEDURES

The study began in the spring of 1972 and continued until the spring of 1974.

Two blinds were set up at the Geneva Colony to allow observation of nesting activity. Both blinds were set up on the east bank of the Geneva pond. One blind was placed opposite trees 1 and 2 about 12 m distant (Fig. 3). Six cormorant nests were visible from this blind. Tree 3, which contained three cormorant nests, was also observable when binoculars were used. The second blind was placed about 300 m farther north near the northeast corner of the pond. Tree 4 was about 30 m away, and nine cormorant nests were observable when binoculars or a spottingscope were used.

All trees were mapped, and each nest was assigned an identification number. In order to determine reuse of old nests and the number of new nests built, the nests that remained intact from the previous year

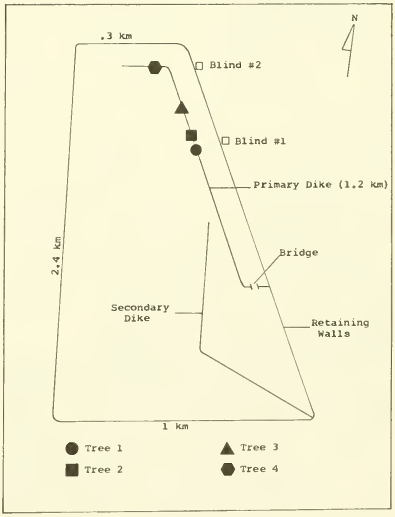

Fig. 3. Map of Geneva reservoir showing the location of the blinds and the trees containing cormorant nests.

were mapped before the birds returned. Observations of the eggs and young in the nests were made using four aluminum poles, 1.5 cm in diameter and 1.6 m long, which could be inserted into one another and secured by a wing nut. A side-view mirror attached to the end pole afforded a view of the nest. When held at chest level, this assemblage allowed visual access to most nests. Tape was placed at 0.2 m intervals on the poles to measure nest height from ground or water level.

One new and one rebuilt nest were collected from the Springville Colony for faunal examination in Berlese funnels and for comparative measurements of numbers, average thickness, and length of each piece of nesting material. Invertebrates found in the nests were collected for identification.

Egg length and width were measured using dial calipers accurate to one-twentieth (.05) of a millimeter. Measurements were made to compare eggs of the same clutch, eggs within the colony, and eggs from different colonies. Egg volume was determined using the formula $V = 0.526\ LB^2$, where L = longitudinal axis and B = transverse axis (Romanoff and Romanoff 1949).

Average clutch size was determined for each colony by including abandoned nests, but not unused nests. A nest was considered abandoned if it contained at least one egg at any time, but showed no signs of incubation for one week. Nests that never contained an egg were considered unused.

Hatching success for each breeding pair was determined by dividing the number of hatchlings that survived one day by the total number of eggs laid in the nest, and for the colony by the total number of hatchlings that survived one day by the total number of eggs laid in the colony.

Fledgling success was determined for the Geneva Colony by dividing the total number of fledglings that left the nest by the number of hatchlings that survived one day.

Three measurements—weight, length of bill, and tarsometatarsus—were made daily of the Geneva hatchlings to determine growth rates. A number indicating nest and order of hatching was written on tape and attached to the leg of each bird for identification. Weight was determined using three Sargent-Welch dial spring-balances: a 250 gm balance accurate to 2 gm, a 500 gm balance to 5 gm, and a 2000 gm balance to 10 gm. A small linen bag was attached to the balance hook to hold the bird for weight readings. The bill and tarsometatarsus lengths were measured with a clear plastic 150 mm rule. The bill was measured from the corner of the mouth to the tip of the upper mandible. The tarsometatarsus was measured from the point of articulation below the ankle to its articulation with the middle toe.

In 1973 trips were made to all recorded nesting sites in the state to determine which colonies still existed and to conduct a census of Utah's cormorant population. The colony at Bear River Migratory Bird Refuge was visited in order to photograph the use of an alternative nesting habitat and to determine location and size. Letters were also sent to managers of selected state bird refuges in an attempt to discover new breeding colonies.

RESULTS AND DISCUSSION

Breeding colonies of cormorants in Utah have been reported in Cache, Rich, Millard, Box Elder, and Davis counties. The only published reference to breeding in Utah County was a brief mention of the area as a "former" nesting site (Woodbury et al. 1949). This paper, then, is the first detailed report of the nesting of the cormorant on Utah Lake, Utah County.

On 20 June 1973 I visited the Newstate Gun Club located 4 km west of Bountiful, Davis County, Utah. An unreported cormorant breeding colony was located with nests in Russian olive (*Elaeagnus angustifolia*) trees along the south side of the Burton Canal. About 15 trees, averaging 8 m high, were scattered for 1 km along the canal. They contained 42 active nests with 66 well-developed young. In addition, 23 immature birds were seen swimming in the canal. The trees containing cormorant nests also held a total of 61 Great Blue Heron nests with young. The caretaker of the property reported that the cormorants had nested there since 1962.

Arrival at Nesting Sites.— In 1972 the first birds to return to the Springville Colony were seen on 4 March. Cormorants were first seen at the Bay Colony on 13 March and at the Geneva Colony on 22 March. In 1973 the first cormorants were seen at the Springville Colony on 7 March and on 14 March at the Bay Colony. Three birds, seen on 26 March, were the first to arrive at the Geneva Colony.

Lockerbie (1942) stated that over a period of years the earliest observation dates for cormorants in Utah was 29 March. The earliest that cormorants have been seen at Bear River Refuge is 5 March (Behle 1958). The arrival of cormorants on 4 March 1972 at Springville during this study is the earliest record for Utah.

In 1972 and 1973 the first returning birds encountered inclement weather conditions, and some ice remained on Utah Lake. It is interesting to note that the first birds returned to the Bay Colony a week later than the Springville birds. Yet, all of the birds that nested at the Bay and Geneva colonies returned within four weeks, while birds were still arriving at the Springville Colony and building nests in late May. Since the first cormorants to return to Springville are often subjected to extremely poor weather conditions, their early arrival must provide them with some adaptive advantage. It may be that since it is the largest colony, nesting space is at a premium and the first birds to return are assured of the choicest areas. I observed that those birds that did not return to Springville until May in 1973 were forced to build their nests west of the main cormorant colony.

The reason for the time difference in return to each colony is puzzling. The Bay Colony is subjected to essentially the same type of weather conditions as Springville. Geneva may have somewhat different weather, but the pond is always ice-free so the birds could obtain food at any time. The Bay and Geneva colonies are considerably smaller in numbers of nesting birds than the Springville Colony, so the lack of competition for nesting space may not require an early return.

It may also be that the birds in each colony remain associated at their wintering grounds and return as a group, or that the individual birds are site specific. Color-banding fledglings to determine if they return to the same colony each year may help answer this question.

Nest Construction.—The Double-crested Cormorant utilizes two different nesting situations determined by local conditions. Of the thirteen colonies reported in this paper, seven were ground-nesting colonies and of these only the Bear River Colony is still in existence. Vermeer (1973) stated that cormorants prefer to nest on the ground and nested in trees only after their ground nesting habitat was disturbed. However, this is not always the case, since the birds at Geneva could have nested undisturbed on the dike in association with California gulls, but instead nested in trees.

Most cormorants that nest along the Atlantic coast nest at ground level on islands bare of vegetation (Bent 1922; Lewis 1929; Mendall 1936). Townsend (Bent 1922) found that these island nests consisted of seaweed, kelp, grass, and a few sticks. The nest dimensions averaged 52 cm across by 12 cm deep.

Unlike the flimsy nests described by Townsend (Bent 1922), Lewis (1929), and Mendall (1936), Behle (1958) found that the ground-nesting cormorants at Egg Island built elaborate interwoven nests of sage and greasewood twigs. The twigs averaged 12 to 18 mm thick and 290 to 580 mm long. The nests were built on or near rocks and some of the nest cups were lined with gull feathers. Nests that had been used for more than one season were almost cemented solid with excrement. Cormorants did not nest on the islands at Bear River Refuge until three years after the islands were built (Marshall 1937). At that time rocks were placed at each end of the islands and cormorants then used them for nesting. Yet, Behle (1958), Lewis (1929), Mendall (1936), and Munro (1927) report nesting on bare ground in comparable island situations.

Nest Utilization.— Of the 83 cormorant nests located in the Springville Colony in 1973, 14 (17 percent) of the nests left from the previous year were utilized by the first returning birds. In the entire colony only five nests were destroyed and two abandoned. The height of the nests averaged 5.2 m (range 2.4 to 7.6 m) above the surface of the water. The nests per tree varied from 1 to 11. There did not seem to be any correlation between the size of the tree and the number of nests the tree contained. Nests were still being constructed in the eastern part of the colony during late May.

Of the seven cormorant nests studied at the Bay Colony during the nesting season, none were lost, although two nests were abandoned. The nest height averaged 5.3 m (range 4.3 to 6.4 m). Nests per tree varied from 1 to 3. All nest-building ceased by early April.

In 1972 cormorants nested in four trees on the dike at the Geneva Colony (Table 1). Trees 2, 3, and 4 were all being utilized by 1 April, but tree 1 was not used for nesting until about 10 days later (Fig. 3). Eighteen nests from the previous year were reused, although some were in very poor condition. One old nest in tree 1 was not used, although it seemed in good condition. No nests were abandoned. One nest each in trees 2 and 4 were lost when they fell out of the trees during a storm.

The same trees used for nesting at Geneva in 1972 were occupied in 1973. However, tree 1 was utilized first in 1973, followed by trees 2 and 4, and finally by tree 3. Twenty-four nests remained of the 33 used in 1972. Some of these were in very poor condition and only 11 (33 percent) of them were reused for nesting. Nest height averaged 4.7 m (range from 3 to 7 m). Three unused nests were destroyed during bad weather and another was lost due to robbing of material by cormorants. Two nests that contained eggs were abandoned before hatching. During both years nest construction was finished by early May.

Table 1. Summary of nest utilization at the Geneva Colony indicating numbers of new and rebuilt nests in each tree used for nesting. The number in parentheses indicates the percent of total colony nests each tree contained.

	Tree 1		Tree 2		Tree 3		Tree 4	
Year	new	rebuilt	new	rebuilt	new	rebuilt	new	rebuilt
1972	0	4(12)	3	6(27)	3	3(18)	9	5(43)
1973	0	3(18)	2	0(12)	2	1(18)	2	7(52)

The reuse of old nests requires a comment. Palmer (1962) stated that rebuilding a nest took only two days, compared to four to six days to build a new one. Rebuilt nests were also reported to be much stronger than new nests. Rebuilding generally consisted of adding some material to the top of the old nest. He gave one record of a nest being reused for four years. I know of four nests at Geneva which were reused for at least three consecutive years.

At all of the colonies there appeared to be a limit to the proximity of nests, since, even when there was a suitable site for another nest, none was built closer than about 1 m to another. The average distance between nests at the Geneva Colony was 1.8 m.

Lewis (1929) described inland nests in Arkansas, Minnesota, and Quebec that were located in various species of trees growing on islands or standing in water. The nests were located 0.3 to 22 m from the surface of the ground or water. He reported that the nest dimensions averaged 22 x 48 cm and that there were never more than six nests in one tree. However, Palmer (1962) observed that trees have contained as many as 36 nests and I observed a tree with 11 nests at Springville. The nests consisted of dead twigs, devoid of bark, and the nest cup was often lined with green leaves or grass and gull or cormorant feathers.

I observed that dead twigs from various species of trees were the primary materials used in nest building. However, large pieces of hardstem bullrush were often used. I was not able to identify the tree species used, but I often saw cormorants pick up dead twigs from the ground beneath the same trees they nested in. Large twigs were secured in the crotch of branches and then other twigs were interwoven until the nest was approximately 30 cm high and 40 cm wide. Reused nests tend to increase in size each year, due to the addition of material. The nest cup was lined with finer materials, including leaves and cormorant feathers. Occasionally, parts of live and dead bullrushes were also used to line the nest cup. One new and one rebuilt nest were collected for comparison of building materials. The new nest had materials averaging 312 mm in length (range 150 to 610 mm) and 7.8 mm thick, the thickest being 26.0 mm. The rebuilt nest had materials averaging 333 mm in length (range 170 to 690 mm) and 8.1 mm thick, the thickest being 25.0 mm.

Prior to measuring, the nests were placed in Berlese funnels to collect invertebrates. A beetle (*Dermestes lardarius*) and several flies (*Rhegoclema* sp.) were identified. These invertebrates should not be considered a definitive list of organisms that are found in company with cormorants. They are only examples of what may be found, as I have encountered no other list of this type in the literature.

From my observations in 1972 I concluded that old nests, in good condition, were the preferred nesting habitat of returning cormorants. There was an order of preference from those highest in a particular tree to the lowest. Only after these were occupied were new nests built. Despite this general rule, at Geneva in 1973 new nests were built while old nests were left unoccupied.

There is evidence that the most mature birds arrive at a colony and begin nesting first (Lack 1968, Palmer 1962). If that were true, the higher nests in a colony may have a better hatching success, since the older birds should be more prolific and make fewer nesting errors (Lack 1968, Lewis 1929). To test this, I took the average of all nest heights for each colony and determined the hatching success for the nests situated above the average height as compared to those below the average height. In every instance, the lower nests had a higher hatching success (Fig. 4). This may indicate that the first returning birds are not necessarily the most mature birds, or possibly that the higher nests, which are more exposed to the elements when the adults are disturbed (not shielded by leaves or branches), have a higher incidence of pre-hatching mortality. However, more research is needed since neither of these ideas seems a completely adequate explanation.

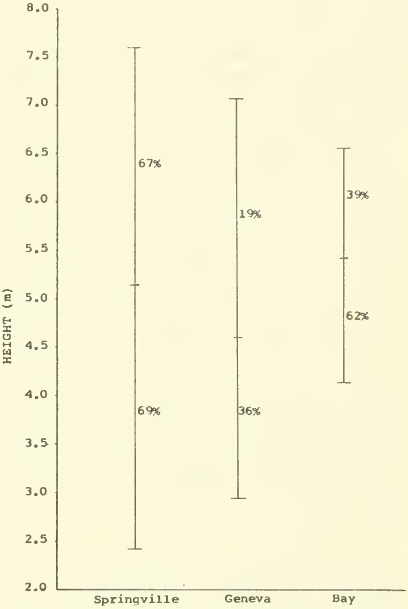

Fig. 4. Distribution of nest height showing hatching success above and below the average nest height.

In Utah it seems to be the rule that cormorants nest in the same trees with Great Blue Herons. Presently in Utah only the cormorants at Bear River do not nest in company with herons. Former nesting colonies in Utah where herons nested with cormorants were located at Bass Pond (Pearson 1927), Cache Valley (Stanford 1937), and Egg Island (Behle 1958). However, this seems to be an uncommon occurrence throughout most of the cormorants' range, since there are few other references to them nesting with Great Blue Herons. Howell (1911), Stoddard (1922), and Vermeer (1973) reported them nesting with herons in Illinois, Wisconsin, and Manitoba, respectively. Ganier (1933) described cormorants sharing a colony with Great Blue Herons, Water Turkeys, and American Egrets in Tennessee. Cormorants have also been reported nesting with Great Blue Herons and Black-crowned Night Herons in Nebraska (Lewis 1931).

I have observed that when cormorants nest in the same trees with herons, the cormorant nests are always located below the level of the heron nests. Stanford (1937) noted the same thing at the colony in Cache Valley. At Springville and Geneva, where only one heron was nesting in a tree occupied by cormorants, the heron's nest was the topmost in that tree. When heron nests were located at the same level as a cormorant nest, the heron nests were never situated closer than 3 m to it. At Geneva in 1972 the highest nest in tree 1 was utilized by a Great Blue Heron. In 1973 the same nest was used by a cormorant, later deserted, and again used by a heron during the same season.

Although there is no explanation in the literature for partitioning of the nesting habitat by these two species, I feel this condition may exist for two reasons. Cormorants are noted for the large amount of excrement they deposit outside the nest, to the point that the very trees they nest in are often killed (Lewis 1929; Mitchell pers. obser.). The feces could also be harmful if they were deposited on heron eggs or young located beneath a cormorant nest. However, the most probable reason is the difference in take-off and landing patterns of the two birds. The cormorant is not an agile bird and, in order to become airborne, must launch itself precipitously out of the nest (Hall 1926). This may result in eggs or young being kicked out of the nest. Likewise, when they land at the nest, they will sometimes miss their footing and fall out of the tree or crash into their nest-mate or other cormorants nesting nearby. In comparison, the Great Blue Heron is able to fly away from the nest with considerable grace by launching itself straight into the air, or land at the nest with amazing agility so as to not disturb any of the nesting birds located nearby. Therefore, I feel that the stratification of the nests of these two species is a behavioral adaptation for partitioning the nesting habitat to avoid interspecific collisions, which could result in the loss of eggs and young.

Further research may answer important questions related to nesting, such as whether cormorants return to the same colony each year or even the same tree and nest. It is not known whether tree-nesting cormorants could effectively become ground nesters. An attempt to induce the ground-nesting cormorants at Bear River Refuge to nest in trees was successful when old nests were placed in nest boxes in an artificial tree made of 2 x 4's on the island in unit no. 4 (Gunther, pers. comm.). It also needs to be determined whether cormorants could be enticed to a new nesting area by taking old nests from a former colony and placing them in a new location.

Egg Laying and Incubation.— In 1973 egg laying began at the Springville Colony on 26 March and continued into late May. Egg laying began at the Bay Colony about 6 April and continued into early May, and at the Geneva Colony began on 13 April and continued until 17 May.

The difference in the beginning egg laying dates at each colony is a reflection of the time differential in early arrivals at each colony. There is a three-week period between the date of first arrivals and the date that eggs are first laid, so that eggs are laid first at Springville and last at Geneva.

The eggs laid on 26 March 1973 at Springville comprise the earliest record for Utah (Behle 1958), although Lewis (1929) stated that Utah had the earliest laying dates for any state and theorized that laying began during the second half of March. Five records from Utah, given by Townsend (Bent 1922), provided dates of 9 April to 17 May for egg laying. The earliest reported date for eggs laid in Utah was 28 March 1937 at Egg Island, Great Salt Lake (Behle 1958). Marshall (1937) reported a very late egg laying date at Bear River Refuge, where nests contained viable eggs on 2 September 1936.

Eggs were laid over a 12-week period at Springville and over more than a 4-week period at Geneva (Fig. 5), although the bulk

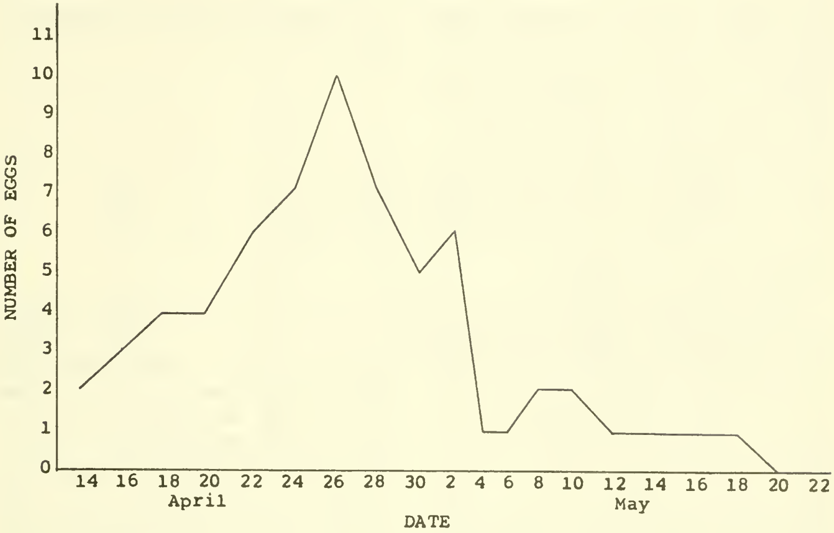

Fig. 5. Distribution of egg laying at Geneva Colony from 14 April to 20 May 1973.

of laying at Geneva came within a 2-week period. Vermeer (1969) reported egg laying lasted for a period of 2.5 months in Alberta, Canada. At Geneva 90 percent of the females laid one egg per day until the clutch was complete. The other females took more than a day to lay one or more of their eggs. Others have noted that females laid one egg per day until the clutch was complete (Behle 1958; Lewis 1929; Mendall 1936), although Lack (1968) stated that cormorants lay eggs every two to three days.

Lewis (1929) and Palmer (1962) reported that incubation usually began after deposition of the third egg. Mendall (1926) and Behle (1958) observed that incubation may begin with the first egg, or at any time thereafter, until the last egg is laid. I found that incubation began immediately after the first egg was laid, which may be due to egg laying beginning early in Utah while the weather is still very cool.

The incubation periods given by Behle (1958), Lewis (1929), and Mendall (1936) were 25 days. Bergtold (1917) reported that most North American cormorants averaged 28 days for incubation, and Worth (1940) gave the incubation period for the European Cormorant (*Phalacrocorax carbo*), though somewhat larger in size than *P. a. auritus*, as 28.5 days. Van Tets (1959), working with the subspecies *P. a. cincinatus* in British Columbia, had 27 records for incubation, varying from 25 to 29 days, with most eggs hatching after 28 days. For the 16 Geneva hatchlings in 1973 incubation varied from 26 to 30 days with an average of 28 days for incubation. The difference between the dates reported by others and my results may again be due to early nesting and cooler weather.

At Geneva in 1972, 11 nests lost one or more eggs before hatching. All of the eggs from four of the nests were lost before 10 May and a replacement clutch was laid for each by 29 May. The replacement clutch consisted of the same number of eggs as lost in three of the nests and one more egg than lost in the other. In 1973, 12 nests lost one or more eggs prior to hatching. However, of the seven nests that eventually lost all eggs, no clutch was completely lost before 24 May, and no new clutches were laid.

Renesting occurred in 30 to 50 percent of cormorants in Manitoba whose eggs or nests were destroyed (McLeod and Bondar 1953). Double-crested Cormorants have never been reported to raise two broods in a single year. It appears that as long as one of the original eggs remains in the clutch, there is no replacement of lost eggs. Also, there is apparently a period during which the female can receive a stimulus that will enable her to lay a new set of eggs. After that time (10 May to 24 May in Utah), she is unable to replace a lost clutch.

Clutch Size.— The normal clutch size of the Double-crested Cormorant is three or four eggs, with four eggs most common (Bent 1922; Davie 1900; Lewis 1929; Mendall 1936). Palmer (1962) reported a range of two to seven eggs with one record of nine eggs. Lewis (1929) found that most cormorants along the Gulf of St. Lawrence had a clutch of four eggs, "rarely" five eggs, and 5–10 percent contained three eggs. Mendall (1936) reported the following percentages for Maine: two eggs, 8 percent; three eggs, 40 percent; four eggs, 50 percent; five eggs, 2 percent. In a census taken on Egg Island, Great Salt Lake, in 1941, Behle (1958) found that over half the nests contained four eggs.

I censused eggs weekly in the Springville and Bay colonies and daily in the Geneva Colony; then the maximum number of eggs present was counted before hatching began. A total of 126 eggs were found in the Springville Colony (average 3.8 eggs per nest), and 28 eggs in the Bay Colony (average 4.0 eggs per nest) in 1973. At the Geneva Colony in 1972 a total of 80 eggs were found (average 4.2 eggs per nest), and in 1973, 61 eggs (3.6 average) were found. The average for all the colonies in 1972 and 1973 was 3.8 eggs per nest. Table 2 indicates the combined totals and percentages of all the clutches from the Utah Lake colonies. These figures agree with other findings, although there is a greater percentage of clutches containing four and five eggs than previously reported.

TABLE 2. Numbers of eggs laid per nest at the Utah Lake colonies. The percent of the totals are in parentheses.

		Number of eggs/nest				
Colony	Year	2	3	4	5	6
Geneva	1972	0	3	10	5	1
Springville	1973	2	6	21	4	0
Bay	1973	0	2	3	2	0
Geneva	1973	1	5	11	0	0
		—	—	—	—	—
	Totals	3 (4)	16 (21)	45 (59)	11 (14)	1(1)

Egg Measurements.— Measurements of the longitudinal and transverse axes of the cormorant eggs indicated that the Bay Colony eggs had the smallest average length and greatest average width of 59.7 x 39.0 (longitudinal x transverse in mm), while the Springville eggs showed the greatest average length and smallest average width of 61.35 x 38.5. The Geneva averages were intermediate in size at 60.43 x 38.99. Small variations from these measurements can be found in the literature as indicated in Table 3, but they are remarkably slight when the large geographic distances separating the samples are considered.

In a discussion on various means of measuring eggs, Preston (1968) stated that measuring all the eggs in a colony produced a bias toward the larger clutches. If measurements are being made in order to establish an average or norm for a species, it is the number of clutches or sets of eggs, not the number of eggs, that is important. He thought that a random selection of one egg from each of 20 or more clutches would be a better indicator for the species. In order to check that hypothesis, I took an average of all the eggs measured at Geneva in 1972 and in 1973. I then compared those averages with three random samples of one egg measured from each of 12 clutches during each year (Table 4). T-tests (two-tailed) at 5 percent indicated that the random means were not significantly different from the overall mean. However, since Preston recommends that the comparison be done with 20 or more clutches, significant differences may appear in larger samples.

Egg Volumes.— Volumes for the eggs measured at Geneva in 1972 and 1973 were calculated in order to establish an average

TABLE 3. Egg measurements from various sources compared with those of the Utah Lake colonies, showing range in length and width measurements with averages in parentheses.

Date	Location	Sample Size	Length (mm)	Width (mm)	Source
–	U.S. Nat. Museum*	40	56.00-65.42 (61.60)	36.50-42.00 (38.80)	Bent 1922
–	Canada	50	54.50-66.50 (59.90)	34.50-42.00 (37.70)	Lewis 1929
–	Maine	15	-------------- (60.50)	-------------- (37.60)	Mendall 1936
–	Egg Island, Utah	20	53.00-64.00 (59.30)	34.80-39.40 (37.10)	Behle 1958
	Total	125	Mean (60.33)	Mean (37.80)	
4/16/71	Bay	7	58.06-60.51 (59.70)	38.17-40.38 (39.00)	White, pers. comm.
4/27/71	Springville	7	58.34-64.05 (61.52)	35.47-41.33 (38.20)	White, pers. comm.
5/18/72	Geneva	48	56.80-63.90 (60.34)	36.90-41.00 (38.93)	This study
5/2/73	Springville	10	58.08-64.52 (61.18)	37.17-40.08 (38.86)	White, pers. comm.
5/8/73	Geneva	52	56.05-65.50 (60.52)	35.40-40.80 (39.05)	This study
	Total	124	Mean (60.65)	Mean (38.80)	

*These were probably collected from Minnesota, North Dakota, Manitoba, Saskatchewan, and Quebec.

for *Phalacrocorax auritus*, since no information on egg volumes for this species was reported in the literature at that time. The volumes were calculated by using the formula Volume = $0.526LB^2$, where L = longitudinal axis and B = transverse axis (Romanoff and Romanoff 1949). The mean volume for the 48 eggs measured at Geneva in 1972 was 48.09 ± 2.80 cc, with a range of 41.55 to 52.69 cc. The mean volume for the 52 eggs measured at Geneva in 1973 was 48.60 ± 3.89 cc, with a range of 38.00 to 54.24 cc.

TABLE 4. Average length and width measurements of all eggs measured at the Geneva Colony in 1972 and 1973, compared to random samples of one egg from each of 12 clutches.

Year	Sample	Length(mm)	Width(mm)
1972	Overall mean	60.34	38.93
1972	1st random sample	56.67	39.18
1972	2nd random sample	60.38	38.74
1972	3rd random sample	60.69	38.94
1973	Overall mean	60.52	39.05
1973	1st random sample	60.08	39.06
1973	2nd random sample	60.55	39.26
1973	3rd random sample	60.67	38.92

Romanoff and Romanoff (1949) have stated that the volume (V) for an egg can also be calculated if the weight (y) is known by the equation $V = 0.913\ y$ for precocial birds and $V = 0.959\ y$ for altricial birds, such as the cormorant. This seems a very unreliable method, since cormorant eggs have a tendency to lose weight after they have been incubated for a time. Rahn and Ar (1974) reported that during incubation all bird eggs may lose approximately 18 percent of their initial weight. The average weight for 12 unincubated cormorant eggs was reported to be 46.9 gm, while 21 incubated eggs averaged 46.2 gm (Lewis 1929).

As a further check on the reliability of this method, I calculated the volumes of 20 eggs, for which the weight was known, and listed the volumes computed for each egg by using both methods (Table 5). The average weight of all the eggs was very close to the average of 46.5 gm for 50 eggs weighed by Lewis (1929). However, there is a difference of almost 4 cc between the average volume calculated from length and width measurements and the average volume calculated by weight. A T-test (two-tailed) at 5 percent indicated that there was a significant variation between these means. Further

TABLE 5. A random selection of 20 eggs, taken at different times and from different Utah Lake colonies, showing the volume as figured by length and width measurement compared to volume computed from weight. (Arranged according to increasing weight.)

No.	Width (mm)	Length (mm)	Weight (gm)	Volume [a] (cc)	Volume [b] (cc)
1	35.47	58.54	37.61	38.59	36.07
2	38.33	60.10	42.03	46.44	40.30
3	38.72	58.08	42.45	45.80	40.71
4	38.17	58.06	42.58	44.60	40.84
5	37.62	58.34	42.62	43.35	40.87
6	38.99	58.87	43.39	47.12	41.61
7	37.17	62.74	43.54	45.64	41.75
8	39.11	59.63	44.78	47.93	42.95
9	37.43	59.43	44.84	43.70	43.00
10	38.85	59.37	44.93	47.28	43.09
11	38.01	64.05	45.40	48.69	43.54
12	38.53	61.96	45.79	48.34	43.91
13	39.21	60.08	47.50	48.50	45.55
14	39.86	59.88	48.16	50.16	46.18
15	39.73	64.52	49.58	53.47	47.54
16	38.92	62.97	49.64	50.15	47.60
17	41.33	61.92	50.86	55.54	48.77
18	39.86	61.59	51.74	51.58	49.61
19	40.08	60.48	52.05	51.17	49.92
20	29.16	61.14	52.79	49.39	50.63
Means	38.73	60.59	46.11 ± 4.05	47.87 ± 3.81	44.22 ± 3.87

[a] Volume as computed by formula; Volume = 0.526 length x breadth^2.

[b] Volume as computed by formula; Volume = 0.959 x weight.

evidence of the unreliability of using weight to calculate volume is evidenced by comparing samples #18 and #20 (Table 5). Although sample #20 is smaller in both dimensions, it weighs over 1 gm more than sample #18. Therefore, the formula given by Romanoff and Romanoff (1949) for calculating volume from the weight of the egg (V = 0.959 y for altricial birds) may hold true for some species, but is not accurate for the Double-crested Cormorant.

Recently, Pagnalli et al. (1974) reported a mean volume for eight Double-crested Cormorant eggs from Maine as 45.87 ± 2.75 cc. Their method involves tracing a profile of the egg and dividing the tracing into segments, then calculating the surface area of each segment, and from that the volume. However, they appear to be working with a somewhat larger bird, since they report a mean egg weight of 49.88 ± 3.37 gm, and I found a mean of 46.11 ± 4.05 gm. The length of the eggs was also different since they reported a mean length of 6.19 ± 0.21 cm and mine were smaller at 6.04 ± 0.19 cm.

Additionally, Preston (1974) has recently stated that the volume of an egg cannot be accurately calculated on the basis of length and width measurements alone without errors of 5 percent or more commonly occurring. Because the cormorant egg is pointed at both ends and describes the shape of a bicone, the coefficient given by Romanoff and Romanoff (1949) would be too large. Therefore, my values for volumes would be overestimated and may result in the difference between my data and those of Pagnalli et al. (1974).

Hatching.— Hatching at the Springville Colony began on 22 April and continued until the second week in June. At the Bay Colony hatching began on 30 April and ended on 27 May. In 1972 hatching began

TABLE 6. Summary of the egg laying and hatching success for the Utah Lake colonies.

Colony	Year	No. Nests	Average Height (m)	Total No. Eggs	Average Clutch Size	Total No. Hatched	Hatching Success
Geneva	1972	19	unk.	80	4.2	44	55%
Springville	1973	33	5.2	126	3.8	83	66%
Bay	1973	7	5.3	28	4.0	15	54%
Geneva	1973	17	4.7	61	3.6	18	30%

at Geneva on 19 May and continued until 10 June. In 1973 hatching began on 20 May and lasted until 9 June. Clutch size, total number of eggs laid, and hatching success are presented in Table 6.

The hatching dates reported for each colony reflect an average of 28 days for incubation. The earliest hatching began at Springville on 22 April 1973 but, owing to the extended arrivals of new birds, lasted well into June. There was a remarkable synchrony of hatching periods at Geneva during 1972 and 1973. In 1972 hatching began on 19 May and continued for 21 days, while in 1973 hatching began one day later and lasted 20 days (Fig. 6). Two to four days are usually required for the complete hatching of a single clutch since incubation starts soon after the first egg is laid (Mendall 1936). Hatching of the first and last bird may be separated by as much as a week or more (Palmer 1962). When this is the case, the youngest birds do not usually survive.

Ricklefs (1969) stated that the hatching success for most colonial nesting birds should be over 50 percent. There is no report of hatching success for *P. a. auritus*, but a record for *P. a. cincinatus* revealed a hatching success of 60.4 percent (Drent et al. 1964). The hatching success at Springville Colony (66 percent) and Bay Colony in 1973 (54 percent), and Geneva Colony in 1972 (55 percent), provided an average of 58 percent (Table 6). That is probably a fair indicator for this subspecies, although the hatching success for ground-nesting cormorants may vary considerably from that value, due to other external factors. The very low hatching success at Geneva in 1973 (30 percent) requires some explanation other than predation. I believe that the daily visits I made to Geneva, in combination with the cool weather during incubation, may principally account for the low success. In order to complete my daily counts, it was sometimes necessary to keep the adults

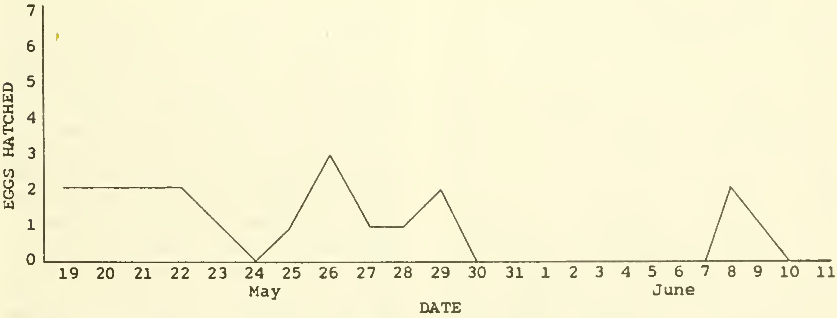

Fig. 6. Distribution of egg hatching at Geneva Colony from 19 May to June 1973.

from the nest for as long as 45 minutes, although the interval was usually less. While awaiting my departure, the adults flew to the reservoir and when I left immediately flew back to the nest. Their moist feathers and water on the eggs may have resulted in an extended period before optimum incubation temperature was again reached (Lack 1968).

Ricklefs (1969) has stated that high temperature in eggs, caused by exposure to the sun, is a serious mortality factor. This may have contributed to the mortality of some of the eggs in exposed nests, but may not be an important factor, since temperatures were not high until the last of May, when 90 percent of hatching was already completed.

Seven of the Geneva nests that were regularly attended by the adults in 1973 contained only addled eggs and made up 39 percent of all Geneva eggs. That is considerably higher than the 24 percent of addled eggs reported for a colony of ground-nesting cormorants (*P. a. cincinatus*) in British Columbia (Drent et al. 1964). All nests at Geneva that contained only addled eggs were still being incubated by the adults two weeks after the expected hatching date. Three of these nests were still being incubated 30 days after the estimated hatching date. Incubation of addled or infertile eggs by cormorants beyond the normal incubation period is well documented (Snow 1960).

Predation of Eggs and Young.— Predation on the eggs and young of cormorants is common. Ferry (1909) observed predation by Ring-billed Gulls (*Larus delawarensis*) on the eggs of cormorants in Saskatchewan. Lewis (1929) reported predation on eggs and young by Great Black-backed Gulls (*Larus marinus*), crows (*Corvus brachyrhynchos*), and ravens (*Corvus corax*). This only occurred when the adults were absent from the nests, since they are usually intrepid defenders of their nests. Herring Gulls (*Larus argentatus*) have also been observed attacking eggs and young of unguarded cormorant nests (Bourget 1973; Mendall 1936). At Mandarte Island in British Columbia, crows and gulls removed eggs from nests that had been vacated for only a few minutes (Drent and Guignet 1961, Van Tets 1959), and 28 percent of the eggs in the colony were lost due to these predations in 1963 (Drent et al. 1964). California Gulls are known to attack and consume the eggs and young of unguarded nests (Behle 1958, Odin 1957, Vermeer 1970). The personnel at Bear River Refuge informed me that they had to employ methods to discourage gulls from nesting because they were so destructive to the eggs and young of water birds, including the cormorant.

There are no records of mammalian predators on the eggs and young of cormorants. Lewis (1929) reported that, even when there were large numbers of coyotes (*Canis latrans*) in an area where a nesting colony was accessible, they were never known to attempt any attack.

Contrary to these reports and the statement made by Armstrong (1965) that gulls always attack eggs in vacated cormorant nests, I never observed mammalian or avian predation at any of the Utah Lake colonies. In addition, I never saw any evidence of predation, such as broken eggs, ravaged young, etc., which would indicate attacks during my absence, although I anticipated serious problems from the California Gulls when I disturbed the nesting birds at Geneva. But even when I kept the cormorants from their nests for as long as 45 minutes, I never observed an aggressive act toward the eggs or young from a gull, although hundreds were flying nearby. It is not suggested, however, that the gulls never attack cormorant eggs and young in this area.

Food Items.— Most of the studies dealing with the food of the Double-crested Cormorant have been along the Atlantic coast (Lewis 1929; Mendall 1936). Therefore, they contain lists of marine species of fish and do not provide good information on the food habits of inland cormorants. The few records that do exist include those of the Biological Survey (Lewis 1929) that reported the stomachs of nine birds collected at the mouth of Bear River contained the following: carp (*Cyprinus carpio*), 73 percent; Utah Sucker (*Catostomus ardens*), 19 percent; Chub (*Leuciscus lineatus*), 3 percent; Chub (*Leuciscus* sp.), 6 percent. Behle (1958) found the following species regurgitated by young birds at Egg Island, Great Salt Lake: carp, catfish, Yellow Perch (*Perca flavescens*), Silverside Minnows (*Richardsonius hydrophlox*), and Webug Suckers (*Catostomus fecundus*). Other records (Lewis 1929, Mendall 1936) have reported cormorants eating Bluegill Sunfish (*Lepomis pallidus*), Pumpkin-seed Sunfish (*Lepomis gibbosus*), Northern Crappies (*Pomoxis sparoides*), Common Crappies (*Pomoxis annularis*), Northern Pike (*Esox lucius*), Walleye (*Stizostedion vitreum*), and a mudpuppy (*Necturus maculosus*). Palmer (1962) recorded crayfish, frogs, Fathead Minnows (*Pimephales promelas*), and dace (*Rhinicthys* sp.) as additional food items.

Food items were obtained only from nestlings that regurgitated when I approached or handled them. Some items that had been partially eaten were taken directly from the nest. Remains of Black Bullhead (*Ictalurus melas*), Carp, and Utah Chub (*Gila atraria*) were found at all three colonies; Goldfish (*Carassius auratus*) were found only at Geneva Colony, and White Bass (*Roccus chrysops*) only at the Springville Colony. The fish found ranged in size from 3 cm (goldfish) to 22 cm (bullhead).

Of these five species of fish the nestlings were known to use for food, the Utah Chub, White Bass, and Goldfish are reported here for the first time.

Development of the Young.— When the young birds hatched they were naked, blind, and barely able to move, and they had a taut black skin, although Lewis (1929) and Mendall (1936) reported that they had a dark-brown skin that turned black within a day or two. From about the fourth day after hatching (Table 7), the oldest birds in the clutch were very aggressive. This sometimes resulted in the smaller or younger birds being deprived of food and ultimately dying of starvation (Behle 1958, Hall 1926). At Geneva three birds apparently starved when only a few days old while their siblings grew normally and continued in good health.

Although starvation may be the major cause of death of fledglings, very young birds are also susceptible to death by exposure during hot weather. On hot sunny days it was necessary for the adults to shade the young, and I have observed the young die within minutes when the adults were frightened away. Of the 18 young that hatched at Geneva in 1973, 13 survived long enough to leave the nest. After they were a week old, the birds were better able to move into shade and employed gular flutter to cool themselves as indicated by Bartholomew et al. (1968) and Lasiewiski and Snyder (1969).

TABLE 7. Reactions to human handling by Double-crested Cormorant nestlings during specific age periods.

Age (days)	Reaction
1-3	Can barely hold head up; no physical resistance or escape attempts; cower and shiver when held; usually make no sound; crawl toward shade when exposed to sun.
4-7	Head held erect to peer at intruder; make a whining sound; cower when hand reached out; attempt to hide behind nest-mates; sit quietly when head or eyes are covered.
8-13	Defecate or regurgitate food when handled; peck at intruders; squawk loudly; peck at nest-mate when placed back in the nest; quiet down when head is covered.
14-22	Climb out of nest onto limbs away from intruder; defecate or regurgitate when approached; use toes and beak to hang onto any object within reach; will not remain quiet even when head covered; peck viciously when handled.
23-	Climb frantically out of nest when approached; often fall or jump out of nest into water; swim well at first attempt.

The eyes opened when the birds were about four to five days old and the egg tooth dropped off at four to seven days, although some birds retained the egg tooth for as long as 12 days. A fine black down appeared about the sixth day. Eight days later the birds were completely covered by down. When two weeks old, the young were very adroit in the use of beak and feet for grasping. When taken out of the nest, they would grab onto anything with their beak and toes, and it was difficult to dislodge them. I observed a four-week-old bird climb 5 m up a tree to the nest from which it had fallen.

Until about two weeks old, the young were fed a semiliquid diet by regurgitation from the adults. Thereafter, whole or partially digested fish were brought to the nest. At 17 to 19 days the flight feathers first appeared along the alar tracts, and the light-colored gular pouch became a deeper yellow. The young were fully feathered at eight weeks and were easily recognizable on the water or in flight by their brownish backs and cream-colored breasts, in contrast to the glossy black of the adults.

Measurements of the Young.— Three measurements of the nestlings in accessible nests at Geneva Colony in 1973 were taken in order to determine growth patterns. Due to the low hatching success, only 16 young were available for measurements and three of those died within four days. Each bird was weighed daily and linear measurements of the beak and tarsometatarsus taken. Figures 7, 8, and 9 contain summaries of these measurements.

The average weight at hatching was 36 gm (Fig. 7), and tarsometatarsal length was 11 mm (Fig. 8). This is close to Lewis's (1929) measurements of 37 gm and 12 mm, respectively. Mendall (1936) reported an average weight at hatching of 32 gm. The average beak length of the Geneva birds at hatching was 17 mm (Fig. 9), but Lewis (1929) reported an average length of 11 mm. The discrepancy is due to different measuring techniques. I measured along the side of the beak from the corner of the mouth to the tip of the upper mandible, and Lewis measured from base to the tip along the top of the beak. The average weight for Mendall's (1936) birds at five days was 158 gm, and mine averaged 156 gm. At 14 days Lewis (1929) reported an average weight of 778 gm, Mendall reported 785 gm, and mine averaged 736 gm. At 20 days the Geneva young averaged 1158 gm; Mendall (1936) recorded an average of 1232 gm. The average weight for the Geneva young after the 23-day period was 1543 gm (Fig. 7). Considerable weight addition takes place thereafter, since Lewis (1929) gave the average weight for adult males as 2100 gm and adult females as 1670 gm. Those values differ from birds collected in Maine where 10 adult males averaged 2233 gm and 12 adult females averaged 1861 gm (Kury 1968). The Utah birds are even larger than those in Maine. Four specimens taken from Springville in 1974 averaged 2247 gm for two females, and 2553 gm for two males.

Other than the averages recorded at hatching, there is no additional information for beak measurements and tarsometatarsal growth in the literature. When 23 days old, the young had an average beak length of 73 mm and an average tarsometatarsal length of 58 mm. Palmer (1962) records the average tarsometatarsal length of adult birds as 61 mm. Measurements of an immature cormorant (BYU Life Sciences Museum) indicated a beak length of 89 mm and tarsometatarsal length of 58 mm. The relationship of these measurements to the growth patterns values are indicated in Figs. 8 and 9. The growth curve of the beak indicates continual increase through the 23rd day, but the tarsometatarsal length levels out at approximately 57 mm after the 19th day.

Nest Departure.— There is little agreement among authors as to when young cormorants first leave the nest and how they accomplish their departure. Some, but not all, of the variation can be explained by the difference in nest location, such as nesting on low islands, on cliffs, or in trees. Townsend (Bent 1922) noted that the young remained in tree nests until fully feathered and flew at about eight weeks of age. However, if they fell into water before they could fly, they would make no attempt to swim. Lewis (1929) reported that the young stayed in tree nests until about six weeks old, when they made their first flight. Mendall (1936) observed that young birds flew feebly to the water from cliff nests at six weeks of age, but were not able to dive until seven weeks old. Lack (1968) stated that cormorants remained in the nest until they could fly and did not swim until after they were able to fly. Cormorants on Egg Island, Great Salt Lake, were observed to swim and dive long before they were able to fly, although no age was noted for either event (Behle 1958). In contrast, Burns (1921) found that the young usually fell, rather

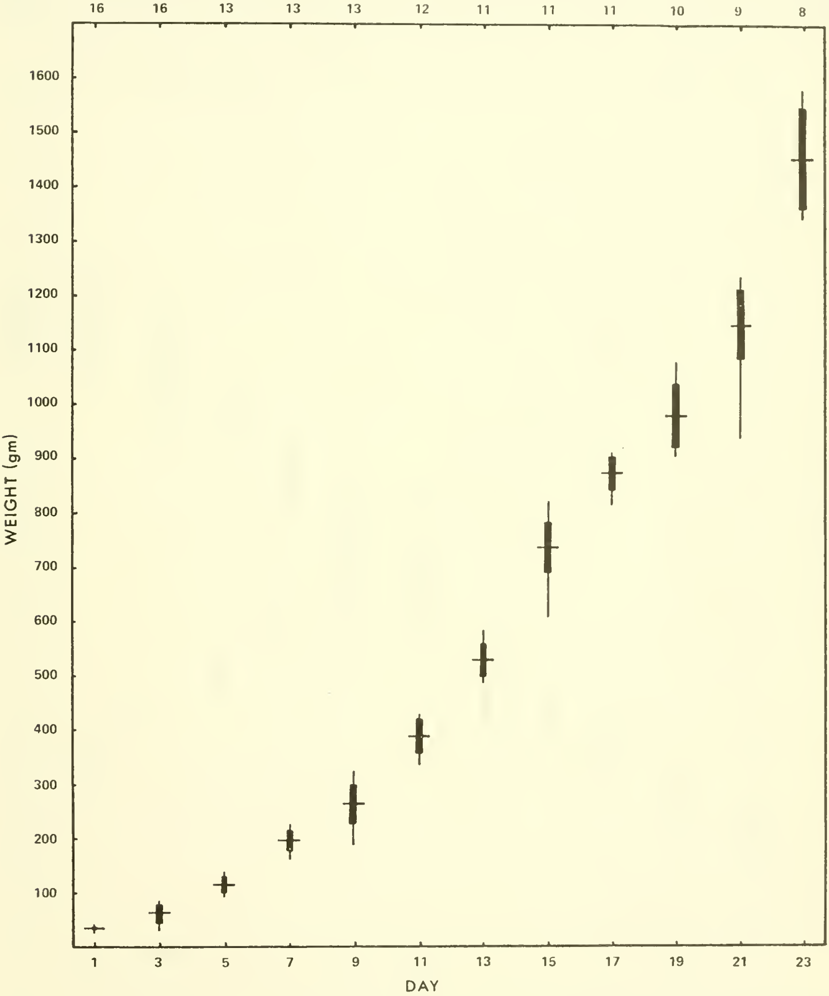

Fig. 7. Mean increase in weight (gm) from measurements on alternate days. The vertical line represents the range, the horizontal line the mean, and the blackened area is equal to two standard deviations. The sample size is given at the top of each day's measurements.

than flew, into the water from nests in trees. Some of these birds were only 17 days old when they fell from the nests.

I observed that very few tree-nesting cormorants in Utah remained in the nest until they were able to fly. After the young were approximately three weeks old, they would leave the nest and move onto tree limbs in order to increase the distance between them and me, which often resulted in young birds falling into the water. At first I suspected that they had drowned, but I later observed them swimming as far as 15 m underwater. After a large number had fallen out of the nest they could be seen swimming in groups some distance from the colony. I presumed

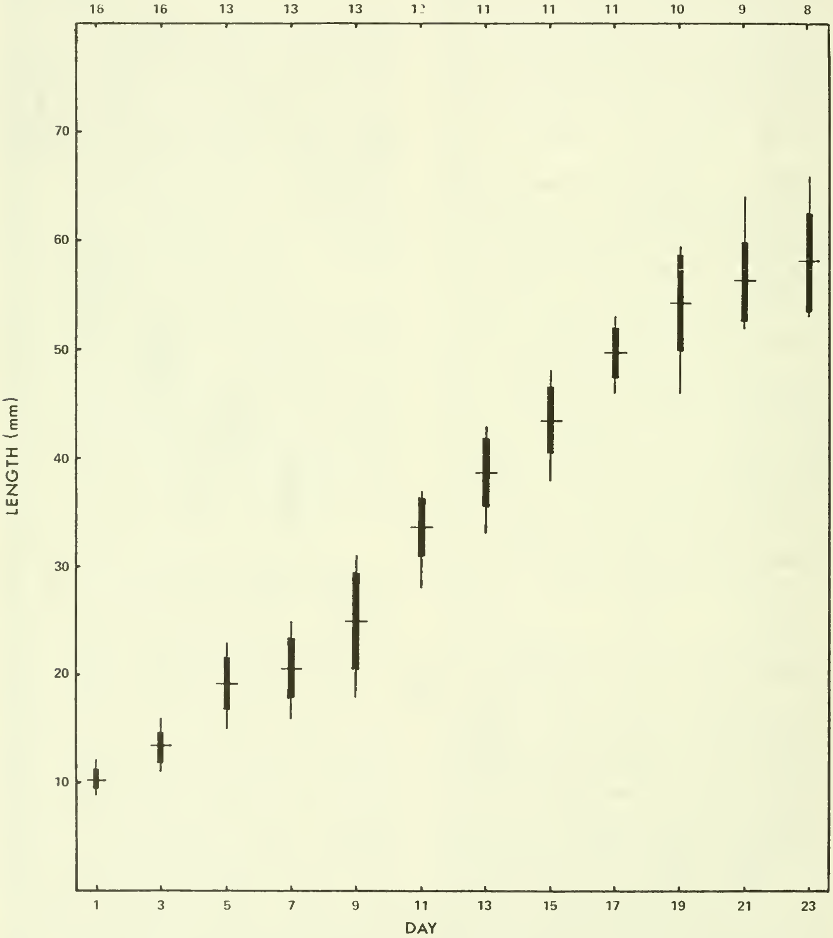

Fig. 8. Mean increase in tarsometatarsal length (mm) from measurements on alternate days. The vertical line represents the range, the horizontal line the mean, and the blackened area is equal to two standard deviations. The sample size is given at the top of each day's measurements.

that my presence caused early departures until I visited the colony at Newstate Gun Club in June 1973. At the time of my visit the birds had not been disturbed for three weeks, yet when I arrived at the colony there were 23 immature birds between three and six weeks of age swimming in the canal. I satisfied myself that they were not able to fly by chasing them up and down the canal. While I was there, other young fell into the water and two birds that fell onto the ground immediately walked over

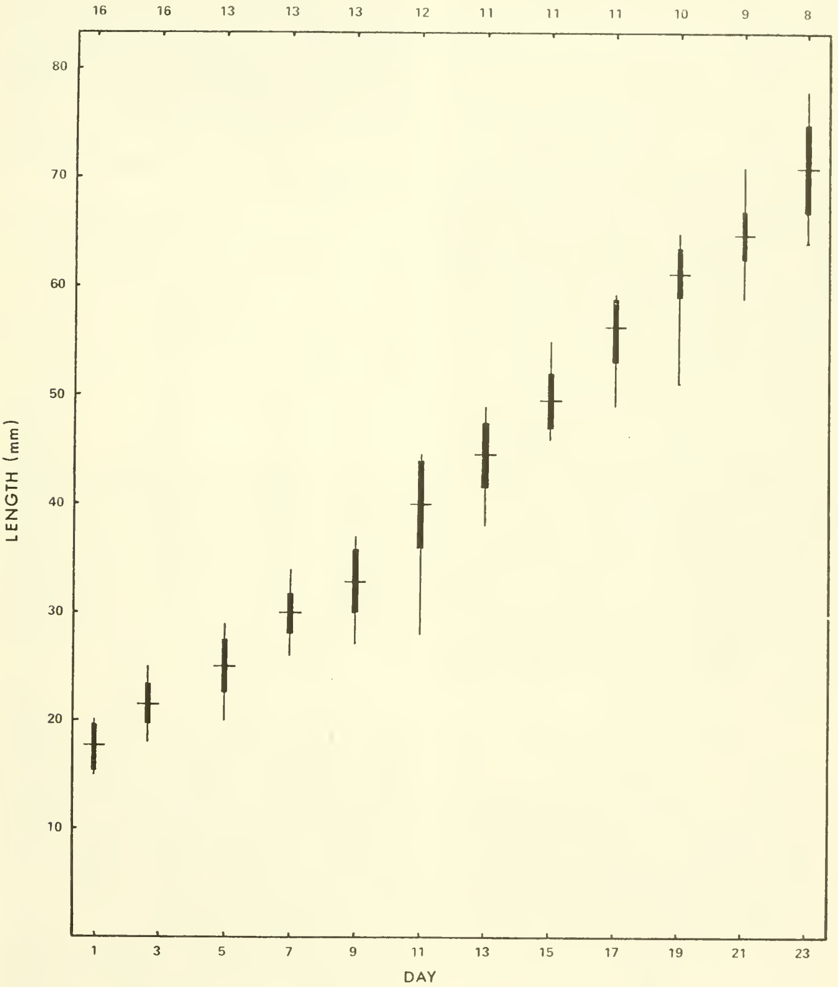

Fig. 9. Mean increase in beak length (mm) from measurements on alternate days. The vertical line represents the range, the horizontal line the mean, and the blackened area is equal to two standard deviations. The sample size is given at the top of each day's measurements.

to the canal and swam away. Early departure from the nest would require the young to learn quickly to fish or to continue to be fed by the adults (Behle 1958, Lewis 1929, Mendall 1936). I have never observed young cormorants being fed on the water, but I assume the adults continue to feed them until they are able to fish effectively for themselves.

The dates stated below pertain to the time when the birds were sufficiently developed to be absent from the nest and probably survive. This does not imply that the birds were able to fly when they left the nest. In all observed cases the birds fell or jumped from the nest into the water and swam expertly away. This made it impossible to estimate the date when the fledglings were able to fly. The earliest date at which birds were absent from the nest at Geneva in 1973 was 17 June, and the last nestling left on 5 July. Age at the time of leaving was between three and six weeks. The oldest bird to leave was 37 days old and the youngest was 21 days old. The average age for leaving the nest was 29 days.

Migration.— Most of the local cormorants leave the Utah Lake area in October. Although I have seen them on Utah Lake as late as 18 November, there is no way to tell if these are local birds or others migrating through. The latest date they have been seen at Bear River is 1 December (Behle 1958). Palmer (1962) stated that almost all of the Atlantic coast migrants have arrived at their wintering grounds in Texas and Louisiana by 1 December.

An unusual sighting was made by Reed Ferris in 1959 (Scott 1959) when he saw a cormorant at Geneva reservoir on 1 January. Since the reservoir is supplied with warm water, it does not freeze during the winter and the bird would be able to fish. However, there was no way to tell whether the bird was a late southern migrant, a bird that had overwintered, a very early arrival, or an injured bird.

Discussion

Status of Utah Lake Colonies.— Provo Bay has been a major nesting site for cormorants for over 50 years (Bee 1920), although it has received little attention. The population there has at times exceeded 300 nesting birds (Bee 1949). Smaller numbers of cormorants have nested in the Geneva Colony but have probably done so continuously for almost 30 years (Bee 1946). The total number of cormorants breeding in the Utah Lake area for the past five years has probably remained stable at around 100 nesting pairs, although the numbers utilizing each colony fluctuate (Table 8).

Table 8. Numbers of active nests in the Utah Lake colonies over a five-year period.

Year	Springville	Bay	Geneva	Totals
1970	Unk.	14	26	Unk.
1971	68	17	18	103
1972	48	12	31	91
1973	83	6	15	104
1974	96	7	0	103

Utah's Cormorant Population.— In 1958 seven cormorant breeding colonies were reported in Utah, but five had been deserted or destroyed (Behle 1958). Behle made no mention of the colonies that were located on White Rock, Great Salt Lake, and Rock Island, Utah Lake, or the existing Utah Lake colonies (Fig. 2). However, the former two sites were limited to a few birds and were probably used only briefly.

In 1974 the only Utah cormorant colonies in use were located at New State, Utah Lake, and Bear River Migratory Bird Refuge. The latter consists of two groups of birds nesting on two small islands, one located in unit four and the other in unit five. Although there is no published reference to nesting since 1949 (Behle 1958), records kept by the refuge personnel indicate continuous usage through 1974.

The population of Double-crested Cormorants in Utah has been steadily decreasing for the past 50 years. Behle (1935) reported a decrease in cormorant numbers on Egg Island from 500 birds in 1915 to 114 in 1935. He felt that the breeding cormorants in the region were threatened with extinction. Sugden (1936) noted an alarming decrease in the numbers of herons and cormorants nesting on the Great Salt Lake and made a plea for their protection.

Of the 13 colonies that have existed at one time or another within the state, only five were still in use in 1974 (Table 9). During the 1930s and 1940s the larger colonies may have easily supported a combined total population of well over 1000 birds. However, in 1973 the total known cormorant population of Utah consisted of only 386 birds nesting in five colonies (Table 10).

TABLE 9. Summary of the populations of Utah's cormorant colonies and their current status.

Colony	Largest recorded no. nesting birds	Year	1973 status
Bear River	600	1947	94
New State	84	1973	84
Geneva	62	1972	30
Springville	166	1973	166
Bay	300	1949	12
Bass Pond	80	1927	destroyed
Bear Lake	400	1929	deserted
Logan	400	1939	deserted
Dolphin Island	150	1919	deserted
Egg Island	500	1915	deserted
Farmington Bay	*2	1951	deserted
Rock Island	*8	1937	deserted
White Rock	*2	1901	deserted

*These are the author's estimates based on the literature.

Effects of Diking Provo Bay.— Two of the five remaining cormorant colonies in Utah are located on Provo Bay, Utah Lake (Fig. 2). In 1973 the Springville Colony was the largest in the state and supported 43 percent of the total remaining birds in Utah and, combined with the small Bay Colony, comprised 178 birds or 46 percent of the state's total cormorant population (Table 10). The proposal to dike and drain Provo Bay as part of the Central Utah Project (Fig. 2) would eliminate the nesting area of these birds.

TABLE 10. Summary of Utah's existing cormorant population as of 1973.

Colony	No. nesting birds	Percent of state total
Springville	166	43
Bear River	94	24
New State	84	22
Geneva	30	8
Bay	12	3
Totals	386	100

Cormorants have been subjected to persecution in the United States and Canada for years. Entire colonies have been wiped out and their numbers reduced by the thousands (Buchheister 1944, Demille 1926, Lewis 1929, McLeod and Bondar 1953, Smith 1911, Stanford 1937). The diking and subsequent draining of Provo Bay will only compound an already critical situation for Utah's steadily declining Double-crested Cormorant population unless adequate measures are taken to protect their present nesting sites.

Acknowledgments.— I appreciate the encouragement and suggestions offered by Dr. Herbert H. Frost during my research and for his critique of this manuscript. I thank Dr. Clayton M. White for his suggestions and critique of this manuscript and Dr. Stephen L. Wood for the identification of insects found in the nests. Appreciation is also extended to the U.S. Steel Company, Geneva Works, for allowing access to the Geneva Colony.

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CATTAIL DECLINE AT FARMINGTON BAY WATERFOWL MANAGEMENT AREA[1]

Christine Minton Anderson[2]

Abstract.— For the last seven years, 1969 to 1976, a steady decline of cattails (*Typha latifolia* L.) has been observed at Farmington Bay Waterfowl Management Area, Davis County, Utah. Several parameters of Farmington Bay's environment that could cause or enhance a decline of the marshland vegetation were studied. These parameters included temperature, pH, phenols, oil and grease, heavy metals, fungus pathogens, and salt water intrusion from the Great Salt Lake. Elevated soluble salt concentrations were found to be responsible for the decline. Cattails are weakened or killed when they are exposed to soluble salt concentrations greater than 5.0 gm/liter, and there is a significant (1 percent level) negative correlation (–0.68) between soluble salt concentration and cattail height. Symptoms of elevated salt concentrations include stunted growth, leaf tip necrosis (burning), and occasional browning of an entire cattail clone. Furthermore, those salt concentrations that cause physiological stress in cattails also facilitate the growth of a decomposition fungus, *Chaetophoma confluens.* This fungus causes a rot consisting of irregularly scattered lesions on the surface of the rhizomes and was consistently isolated from rhizomes of declining plants.

For the last seven years, 1969 to 1976, a steady decline of cattails has been observed at Farmington Bay Waterfowl Management Area, Davis County, Utah. The management area is 4,205 feet above sea level, located on the east shore of the Great Salt Lake, 15 miles north of Salt Lake City. The primary water source is the Jordan River. Water flows northwesterly, and Farmington Bay flows directly into the Great Salt Lake.

At Farmington Bay, cattails in many areas were less than 1 m high, as compared to healthy cattails that frequently attained heights of 2 m. During the summer, cattails appeared to grow normally until July; growth then ceased. Yellowing and necrosis followed rapidly. Older parts of the cattail clones died first, with the younger shoots gradually following the same pattern. Inspection of the rhizomes revealed the presence of mahogany-colored cankers, or lesions, scattered irregularly over the surface. In some cases the lesions had extended deep into the tissues, and some rhizomes had completely rotted away.

These symptoms are characteristic of those caused by soil fungus pathogens, and it was suspected that the lesions might be the result of such a fungus and, in turn, that the lesions might cause the plant's decline. A fungus might act either as a primary pathogen or a weak, secondary pathogen, affecting tissues subjected first to some other stress. If this were the case, it would be necessary to establish what stresses might be involved and to define their relative contribution to the cattail decline.

The objectives of this study were to: 1) determine the cause or causes of the cattail decline; 2) evaluate the seriousness of the situation; and 3) provide information so that corrective or control measures could be developed to protect existing marshland vegetation and reestablish vegetation that had been destroyed.

A fourth objective was to better understand the marsh ecosystem. In this system, decomposition is an ecological factor that may be important in affecting marsh plant interactions. The declining cattails offered an opportunity to study how fresh-water marshlands might undergo decomposition and change.

The broad-leaved cattail (*Typha latifolia* L.) is common to North American marshlands and dominant in Utah's waterfowl management areas. Other common marsh plants are alkali bulrush (*Scirpus paludosus* A. Nels.), hardstem bulrush (*Scirpus acutus* Muhl.), salt grass (*Distichlis stricta* Torr. Rydb.), and salicornia (*Salicornia rubra* A. Nels. and *Salicornia pacifica* Standl.).

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Important as a successional species, the cattail is a plant that traps sediment and nutrients, allowing the subsequent establishment of bulrushes. Bulrushes, the climax species of the marsh, provide abundant waterfowl food. Cattails, on the other hand, have little value as waterfowl food, and, when it is dominant in waterfowl management areas, the cattail is considered a nuisance because its dense stands make it useless as nesting habitat or escape cover. Cattail rhizomes are palatable to humans, muskrats, and geese; the plants themselves are used by waterfowl for nesting and escape cover when their growth has been controlled.

The most significant publication on the subject of Utah marshlands contains the results of 25 years of experimental work at Ogden Bay Refuge, 12 miles west of Ogden, Utah, near the east shore of the Great Salt Lake (Nelson 1954). The purpose of the study was to determine how marshland could be developed and waterfowl populations increased; records were kept to ascertain how plant community changes influenced animal populations. Several of the conclusions were pertinent to the present study at Farmington Bay.

Major factors limiting plant growth and waterfowl use at Ogden Bay included water supply, seasonal water fluctuations, fluctuations of the Great Salt Lake, and overgrazing. Salt tolerance differed among plant species. Of the emergent species, alkali bulrush was the most tolerant; cattail was second. All of the marsh plants were able to tolerate soil salinities exceeding the salinity ranges for agricultural crops. As plant cover was increased, waterfowl populations increased because new nesting areas were created and abundant food was made available.

After vegetation had been developed on the Ogden Bay Refuge, it became evident that cattails, especially in the less saline areas of the marsh, could effectively outcompete other plants. Dense stands, useless for waterfowl nesting, were established. In 1947, cattail control studies were initiated by the Utah State Department of Fish and Game (Nelson and Dietz 1966). The control methods used to experimentally eliminate cattails included cutting, crushing, and mowing; chemical sprays; explosives; fire; and drought. It was concluded that by adjusting the water levels cattail overgrowth could be controlled; when mud flats were not covered with water during the growing season, large-scale cattail invasions occurred.

At Fish Springs, a salt marsh west of Salt Lake City, *Typha angustifolia* (narrow-leaved cattail) does not form large communities (Bolen 1964). Bolen noted that *Scirpus acutus* and *Typha latifolia*, common species of Utah's fresh-water marshes, did not occur at Fish Springs. He concluded from his data that while it was probable that salinity limited the development of these species, water depth or some other factor was probably responsible for their absence at Fish Springs.

In contrast to the Fish Springs study, data on physical and chemical soil constituents at Bear River Bird Refuge indicated that soluble salts affected the yields of aquatic plants. Areas low in soluble salts were more productive than areas high in soluble salts (Jensen 1940). It was determined that high salinity, in addition to affecting vegetative growth, interferes with seed germination and seed production of Utah marsh plants (Kaushik 1963).

Literature published on other localities stresses the importance of soil salinity in interactions between marsh plants (Haller 1974). Salinity is considered to be a primary factor in determining plant distributions in Louisiana marshes; cattails are limited to fresh-water areas of less than 0.5 percent salt (Penfound and Hathaway 1938). Water levels, in addition to salinity, are also thought to determine plant distribution (Bourn and Cottam 1939).

Cattail populations growing in disturbed salt flats have salt tolerances characteristic of each species. A concentration of 1 percent sodium chloride in hydroponic tanks caused stunting, drying, and leaf curl in *Typha latifolia*. *Typha angustifolia* was able to withstand 2 percent sodium chloride concentrations. A hybrid intermediate, *Typha glauca*, had an intermediate salt tolerance (McMillan 1959). Since many terrestrial plants also differ widely in their salt tolerance (Levitt 1972), an effort was made to determine the relationships between cattail decline and salinity at Farmington Bay.

METHODS

Five different features of the problem were studied: 1) the isolation of a possible fungus pathogen; 2) the investigation of environmental stress conditions; 3) the evaluation of marshland by aerial photography; 4) laboratory experimentation on the effects of salinity on cattail growth; and 5) laboratory experimentation on the effects of salinity on the growth of an isolated fungus.

1. Isolation of the fungus: Diseased cattails were collected, and plant tissue was cut from necrotic lesions with a sterile scalpel. The infected tissue was surface sterilized and placed on Difco-Bacto Agar with nitrogen or Difco potato dextrose agar. Plant tissue was surface sterilized with a 10 percent aqueous solution of Purex bleach.

Pure cultures were obtained by transferring the developing fungus mycelium onto fresh agar. Cultures were allowed to grow at room temperature. Slant test tube cultures provided a method of storage, and they were refrigerated until used. The fungi were identified. Fungus mycelium was mounted on temporary slides with a drop of water for most identifications. To aid in the identification of one species (*Chaetophoma confluens*), fixing, sectioning, and staining were used. Tissue was fixed in formalin-aceto-alcohol and embedded in paraffin. Sections, 15 microns thick, were stained with safranin 0 according to the methods described by Johansen (1940).

2. Environmental parameters: Studies were conducted to determine the environment's contribution to the vegetation decline. This included measuring salinity, pH, biological oxygen demand (BOD), dissolved oxygen (DO), and temperature. Samples of soil and water were taken weekly during the months of May through September, 1974. All routine sampling was done at the four sampling sites shown on Figure 1. Cattails appear to be healthy at Site 1 and Site 3. Cattails are in a state of decline at Site 2; Site 4 represents the outlet of Farmington Bay and has no cattails.

Conductivity of both soil extracts and water samples was measured in the laboratory at 25 C with a conductivity bridge (Richards 1954). Then pH was measured to the nearest tenth of a pH unit with a Beckman pH meter. BOD samples were taken once a month and analyzed by the Utah State Division of Health. Water samples for dissolved oxygen were measured weekly in the field according to the azide modification; DO was measured in milligrams per liter and expressed relative to 100 percent saturated water (American Public Health Association 1971). In addition, samples were chemically analyzed monthly by the Utah State Division of Health to determine which industrial pollutants were present. Air and water temperature were measured in the field with a centigrade thermometer. The data obtained were used to calculate the percent of dissolved oxygen in the water. Weather conditions for the summer were recorded and compared with previous summer conditions.

3. Mapping of vegetation: Aerial photographs and moving films of Farmington Bay and the surrounding area were taken. The Ogden Bay Waterfowl Management Area, the Bear River Bird Refuge, and Red Butte Canyon were also examined for indications of vegetation decline in order to determine if the decline was in some way uniquely associated with Farmington Bay. A vegetation map of Farmington Bay was made so that the affected area could be properly illustrated and the extent of damage could be determined. A U-2 infrared aerial photograph (scale 1:120,000) was projected onto a United States Geological Survey Map (Farmington Quadrangle, scale 1:24,000) with a Bausch and Lomb Zoom Transfer Scope. Areas covered by marsh vegetation were traced onto the geological survey map. The U-2 infrared photograph, obtained from the Geography Department at the University of Utah, was taken 14 September 1972 by a high-flying aircraft at about

50,000 feet. Standard infrared film was used in a high-resolution camera. Healthy vegetation is bright red, vegetation under stress is salmon colored, and dead vegetation is white. A compensating polar planimeter was used to determine the area covered by healthy marsh vegetation and the extent of diseased vegetation.

Color aerial photography for assessing the quality of marshlands has just recently come into use. Further information on the methods used in aerial mapping of marshlands can be obtained from Seher and Tueller (1973); the source also explains how infrared photographs should be interpreted. In addition, a bibliography on the use of aerial photography (Anson 1975) has been compiled that provides more detailed information.

4. Laboratory experiments determining effects of salinity on cattail growth: Cattails were grown from seeds gathered at Farm-

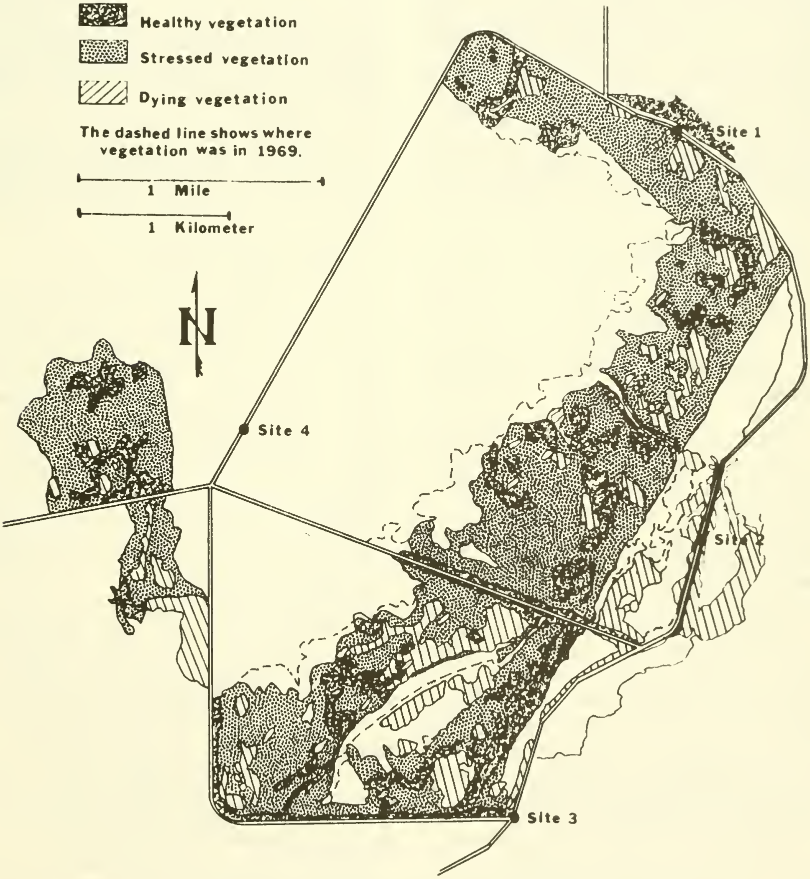
Healthy vegetation
Stressed vegetation
Dying vegetation
The dashed line shows where vegetation was in 1969.
1 Mile
1 Kilometer
N
Site 1
Site 4
Site 2
Site 3

Fig. 1. Farmington Bay Waterfowl Management Area.

ington Bay. Seedlings were transferred to six hydroponic tanks when they were about six inches high; the tanks contained a four-salt nutrient solution made according to the methods described by Arnon and Hoagland (1940). Nutrients were replaced monthly during the experiment. Each of six hydroponic tanks contained 10 individual plants. Two tanks served as the control; the other four tanks were used to determine the effects of different salt concentrations on the cattails. After the seedlings had acclimatized and had shown vigorous growth, sodium chloride was added in small amounts (0.01 Mole per day) over a period of 30 days. This was done to determine a realistic salt tolerance for the cattails without putting them under undue stress. Shoot growth of each plant was measured every two days. The final concentrations at the end of the period of additions were two tanks with 0.0 M sodium chloride, two tanks with 0.1 M sodium chloride, and two tanks with 0.3 M sodium chloride. The cattails in one tank of each salt concentration were inoculated with *Chaetophoma confluens*, the fungus that was most often isolated from the lesions on the cattail rhizomes. Inoculation was performed by injecting a fungus-water suspension into the host with a hypodermic syringe.

Cattail rhizomes were observed throughout the experiment for the development of lesions and other symptoms of stress. When the experiment was terminated, a wet weight for shoots and rhizomes of each plant was obtained. Tissue from all experimental plants was cultured for isolation of the fungi that were present.

5. Effect of salinity on the fungus, *Chaetophoma confluens*: *Chaetophoma confluens* was grown on potato dextrose agar, to which sodium chloride had been added. The following sodium chloride concentrations were prepared: 0.0, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8 M. Cultures of each salt concentration were inoculated with 0.5 cmsquares of mycelium and were allowed to grow for two weeks in an oven held at 30 C. The area covered by fungus mycelium was determined by tracing the area onto paper, cutting, and weighing. The average growth area at each salt concentration was graphed.

RESULTS

Three fungus species were isolated from diseased cattails that had been collected at Farmington Bay. *Fusarium tricinctum* was isolated in 12 (16.2 percent of the isolated fungi) out of 74 fungus isolations. *Botrytis cinerea* was isolated 14 times (18.9 percent). Both of these fungi are saprophytic on decaying plant material. *F. tricinctum* occurs frequently on moldy corn and grain; *B. cinerea* causes "gray mold" of numerous ornamental and crop plants (Barron 1968). Neither of these fungi has been reported to occur on *Typha*.

Chaetophoma confluens was isolated 48 times (64.9 percent). *Chaetophoma* might be an important decomposition fungus in the marsh. It has been isolated from *Spartina* (cordgrass), a common emergent in salt-water marshes (Barnett 1956).

Another fungus, tentatively identified as a species of *Olpidium*, was discovered when the stained sections of cattail rhizomes were examined; the relationship of this fungus to cattail rhizome rot is unclear. Only a few species of *Olpidium* are parasitic on higher plants. When *Olpidium* infects clover or vetch, it causes distortions of the leaves; in one species of grass, *Agrostis stolonifera*, it causes root hair distortion. *Chytridiomycetes* (the fungus class that includes *Olpidium*) are characterized by the production of motile cells and are typically found in aquatic habitats (Sparrow 1943).

The most probable cause of the vegetation decline was revealed when the results of the water and soil analyses were examined. Figures 2 and 3 show the results of the conductivity measurements. The figures show that the salinity increases dramatically during the summer at Site 2, reaching a maximum during the month of July. This peak coincides with the period during which cattail deaths were first observed during the summer. The salinity peak also came just after the Great Salt Lake reached its high of 4,201.30 feet above sea level in June (United States Geological Survey

1975). The 4,205-foot level is shown along the east side of Farmington Bay on a United States Geological Survey Map of the area; the west side of the management area is approximately 4,200 feet above sea level. Apparently, the management area is at the same elevation as are the Great Salt Lake brines for part of the summer. Chemical analyses of the water at Farmington Bay showed that sodium and chloride ions were present in the greatest amounts at this time. It was concluded that these ions made the largest contribution to the measured conductivity values.

To determine the significance of the relationship between salinity and cattail decline, another experiment was conducted. This experiment consisted of taking water samples every tenth of a mile (0.16 km) along the east side of Farmington Bay and along the dike that runs east and west across the refuge. As water samples were taken, the average height of the cattails was recorded in centimeters. Cattails were measured in a circular area of 10 m in diameter. The point where the water sample was taken served as the center of the circle. Average heights were based on measurements of 20 to 50 cattail plants. Only living cattails were measured. Figure 4 shows a graph of conductivity versus cattail height. There is a moderately high, negative correlation (r = –.68 with 41° of freedom) between conductivity and cattail height. These field data also showed that cattails exhibit disease symptoms when the dissolved salt content exceeds 5.0 gm/1.

The pH of Farmington Bay lies between the normal ranges of river water: 5.0 to 9.0. The data showed that there was no correlation between pH and cattail height.

The BOD at Site 2 progressively increased during the summer, while the BOD at Site 3 and Site 4 increased slightly and

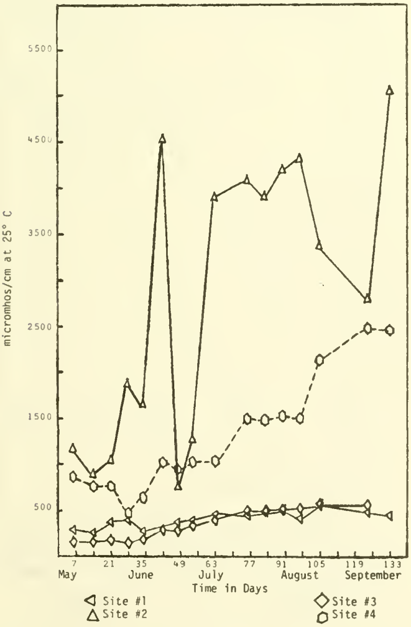

Fig. 2. Conductivity of the water.

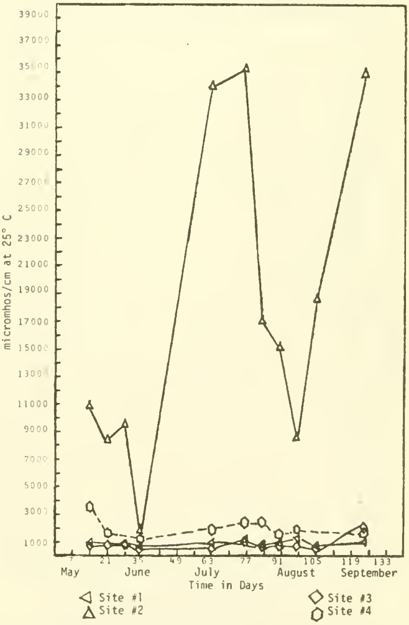

Fig. 3. Conductivity of the soil.

then leveled off (Fig. 5). The large increase indicated that oxidizable organic material was accumulating at Site 2. Results of the DO measurements are shown in Figure 6. Dissolved oxygen at Site 2 got as low as 46 percent saturated. Despite some periods of low DO and high BOD, the dissolved oxygen was high overall during the summer and no detrimental effects were observed that could be related to low oxygen availability.

The results of the chemical analyses showed that the chemical parameters of the water were normal except for the high salinity. Small amounts of phenols, oil, and grease were found in the water, and a discussion of their significance to this study is included in the *Discussion* section of this article.

The effect of sodium chloride on the growth of the fungus, *Chaetophoma confluens*, is shown in Figure 7. The addition of sodium chloride was found to increase growth. Optimum concentration for growth of *Chaetophoma* is 0.30 M sodium chloride. Cattails growing in hydroponic tanks showed symptoms of salt toxicity (leaf burn and wilting) at sodium chloride concentrations of 4.68 gm/l (0.08 M). At sodium chloride concentrations of 17.6 gm/l (0.30 M), growth was completely arrested and rhizomes began to rot. The results correlate well with the results of the field study. Table 1 shows how increased salt concentrations affected the wet weights of shoots and rhizomes.

Attempts to isolate *Chaetophoma* from lesions that developed on cattails following inoculation were unsuccessful. Because of the observed effects of salinity on the cattails, and because *Chaetophoma* was only isolated in two (out of 20) cultures in previous inoculation experiments, it could not be concluded that the fungus was a primary

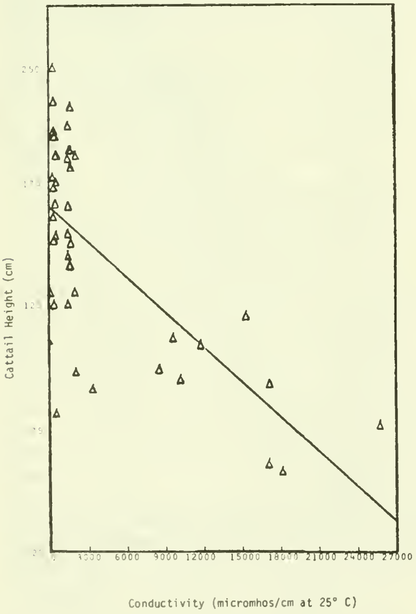

Fig. 4. Conductivity vs. cattail height.

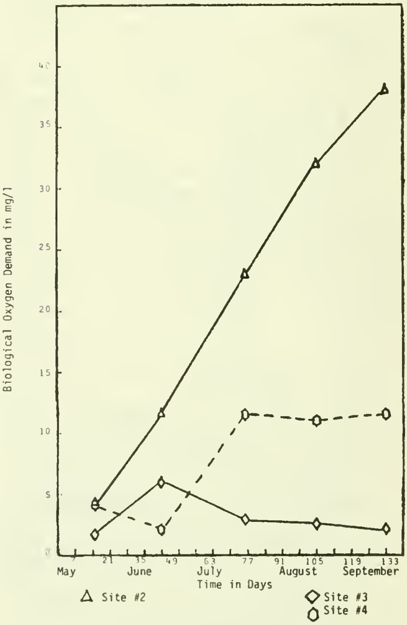

Fig. 5. Biological oxygen demand.

cause of the cattail decline. The combination of the appropriate soluble salt concentration and the fungus appears to be critical in producing the symptoms observed at Farmington Bay. Figure 8 shows that the optimum sodium chloride concentration for *Chaetophoma* growth (0.30 M) corresponds to the salt concentration (0.30 M) that causes cattail death.

TABLE 1. Wet weights of cattail shoots and rhizomes in relation to salinity.[1]

Sodium Chloride Concentration	Rhizome Weight	Shoot Weight	Shoot : Rhizome Ratio
0.0 M	73.0 gm	209.7 gm	2.90 : 1
0.1 M	53.4 gm	58.6 gm	1.10 : 1
0.3 M	26.2 gm	11.1 gm	0.42 : 1

[1] These are the average weights of all the plants that were grown in a given sodium chloride concentration.

DISCUSSION

At present, the vegetation in Farmington Bay and the neighboring duck clubs appears to be under stress. The stress conditions occur throughout the marsh, leaving very few places unaffected. Healthy vegetation is found only in the higher areas of the marsh and where fresh water is flowing in from the Jordan River.

The portion of Farmington Bay illustrated in Figure 1 has an area of 11.88 square kilometers (2,934 acres). Of this, 4.88 km^2 (1,205 acres) is emergent vegetation. In 1969, Farmington Bay had 5.92 km^2 (1,462 acres) of emergent vegetation; 1.04 km^2 (257 acres) of this vegetation has disappeared, and 1.28 km^2 (316 acres) of vegetation is dying and in the process of disappearing. It is interesting to note that in 1959 there were only 1.40 km^2 (346 acres) of vegetation in the portion of Farmington Bay that is illustrated. At the present time,

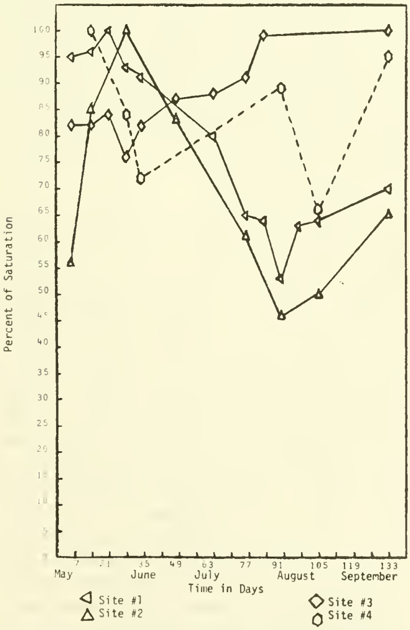

Fig. 6. Dissolved oxygen.

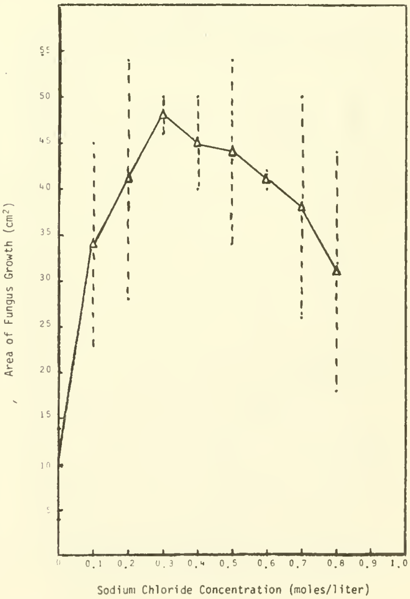

Fig. 7. The effects of sodium chloride on the growth of *Chaetophoma confluens*.

there is more vegetation in Farmington Bay than there was in 1959. The same general pattern of vegetation decline is occurring in the southern portion of Farmington Bay and in the marshland to the south that is not shown in the illustration. The decline appears to be occurring slowly, and it would take several years of similar conditions to eradicate the emergent marsh vegetation.

Several parameters of Farmington Bay's environment could cause or enhance a decline of the marshland vegetation. Among these are adverse temperature ranges, pH, phenols, oil and grease, fungus pathogens, and salt water intrusion from the Great Salt Lake. All of these potential pathogens were examined in this study. The effects that each agent or factor might have on the vegetation, alone or in combination, were considered.

Since no unusual temperature changes have been recorded at Farmington Bay, temperature can be immediately eliminated as the cause of vegetation decline. Marshes in Red Butte Canyon that experience a similar range of air and water temperatures have shown no signs of diseased or dying vegetation. However, the cattails at Farmington Bay are dying during the warmest part of the summer, and it is possible that high temperatures might be enhancing the effects of some other stress to which the cattails have already been subjected.

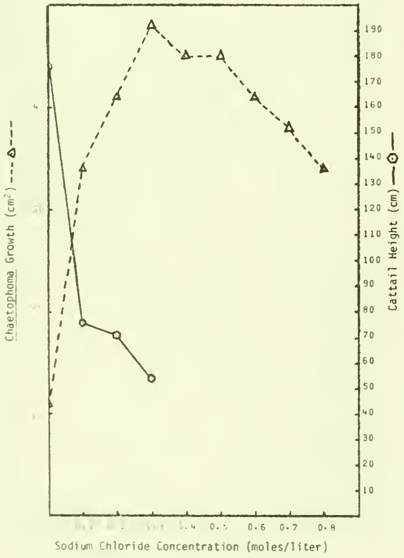

Fig. 8. The effects of sodium chloride on the growth of cattails and *Chaetophoma confluens*.

Soil and water pH greatly affect the availability of plant nutrients. The ideal pH range for most crop plants is from 6.5 to 7.5 (Sprague 1964). Average values above 8.0 or below 5.0 would be necessary to create serious nutrient deficiencies and cause disease. A pH range of 5.0 to 9.0, with an average pH around 8.0, was measured at Farmington Bay. Chlorosis (yellowing of the leaves), which is indicative of many nutrient deficiencies, and other characteristic symptoms that commonly occur in response to the lack of essential elements, were not observed (Treshow 1970). In addition, no statistical correlation could be obtained between pH and cattail growth as determined by height. In other studies conducted on Utah marsh plants, it has been shown that vegetation grows well in the pH ranges that occur at Farmington Bay (Jensen 1940, Nelson 1954, Kaushik 1963). There is little possibility, therefore, that pH is contributing to the vegetation decline.

Analysis of the water at Farmington Bay for possible industrial pollutants revealed the presence of phenols, oil, and grease. Phenolic compounds in water resources are usually a result of pollution from oil refineries. Phenols also result from the breakdown products of herbicides such as 2,4-dichlorophenoxyacetic acid (2,4-D) and 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) (Goerlitz and Brown 1972). The oil refineries upstream from Farmington Bay and the herbicide treatment of some grain crops with 2,4-D are the most probable sources of the phenols, oil, and grease in Farmington Bay. Phenol concentrations ranged from none to 0.008 mg/l. These concentrations are extremely dilute when compared to the concentrations of phenolic compounds (such as 2,4-D) that are known to be toxic to broad-leaved dicots (Crafts and Robbins

1962). Since the concentrations of phenols are dilute, there is little possibility that phenols are causing the vegetation decline. However, phenolic compounds might be contributing to the decline by inhibiting the reestablishment of cattail seedlings. McNaughton (1968) has shown that phenols produced by *Typha latifolia* have an autotoxic effect on seed germination and seedling growth. Oil and grease measurements ranged from 0.6 mg/l to 8.0 mg/l. These concentrations are also too dilute to cause any vegetation damage (Goerlitz and Brown 1972).

Study of the total salt content, or salinity, of the soil and water of Farmington Bay revealed that the existing salinities were in a range that is known to be toxic to many plant species (Richards 1954). Field studies showed that cattails are weakened or killed when they are exposed to soluble salt concentrations greater than 5.0 gm/l. Penfound and Hathaway (1938) have also found that *Typha latifolia* plants in Louisiana marshes do not occur where salinities are above 5.0 gm/l. McMillan (1959) found that *T. latifolia* grown in hydroponic tanks could not tolerate 10 gm/l, and Kaushik (1963) found that cattails from Ogden Bay Waterfowl Management Area were killed when subjected to a soluble salt concentration of 0.9 gm/l. Symptoms of the elevated salt concentrations on cattails include stunted growth, leaf tip necrosis (burning), and occasional browning of the entire plant. Furthermore, the salt concentrations that cause a physiological stress to cattails facilitate the growth of a decomposition fungus, *Chaetophoma confluens.* This fungus causes a rot consisting of irregularly scattered lesions on the surface of the rhizomes and was consistently isolated from rhizomes of declining plants. At the beginning of this study, it was thought that the fungus might be a primary cause of the decline. However, elevated soluble salt concentration appears to be the primary cause.

The source of the elevated salt concentration at Farmington Bay is undoubtedly the Great Salt Lake. Salinities in Farmington Bay increase and decrease following the rising and falling of the lake. Salinity measurements of the water entering Farmington Bay from the Jordan River show concentrations of salt between 0.1 gm/l and 0.6 gm/l. These concentrations do not seem to be increasing the salinity of Farmington Bay. The Great Salt Lake, on the other hand, with a salt concentration of 224 gm/l, is a natural source of salt for bordering marshlands because the brines are known to diffuse through and under the dikes around the marshes. The periodic fluctuations of the Great Salt Lake allow for a natural control of the density of cattail stands. This could be either beneficial or detrimental, depending on the frequency and extent of the fluctuations. In order to maintain a desirable stand density, it is suggested that the salinity be monitored and controlled.

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OSTEOLOGY AND MYOLOGY OF THE HEAD AND NECK REGIONS OF *CALLISAURUS*, *COPHOSAURUS*, *HOLBROOKIA*, AND *UMA* (REPTILIA: IGUANIDAE)

Douglas C. Cox[1] and Wilmer W. Tanner[2]

Abstract.— A detailed study of the anterior osteology and myology of *Callisaurus*, *Cophosaurus*, *Holbrookia*, and *Uma* reveals the phylogenetic relationships among the sand lizards. An SPSS discriminant analysis of osteological characters combined with myological characters indicates that *Callisaurus* is most primitive, *Cophosaurus* and *Holbrookia* are most closely related, and *Uma* is the most distinct of the sand lizard genera. Because of close relationships between *Cophosaurus* and *Holbrookia*, it is postulated that earlessness evolved once, and *Cophosaurus* is returned to synonymy under *Holbrookia*.

Blainville (1835) wrote the first description of a sand lizard and named it *Callisaurus draconoides*. Since then various authors have published articles concerning sand lizards. Girard (1851) described *Holbrookia maculata*, Trochel (1852) described *Cophosaurus texanus*, and that same year Baird and Girard synonymized *Cophosaurus* with *Holbrookia*, providing the name *Holbrookia texana*, which then remained unchanged for over 100 years. Subsequently, Baird (1858) described *Uma notata*.

By 1858 all genera represented in the sand lizard group had been described. Since then new species and subspecies, as well as new combinations, have been added by various authors as follows: Bocourt (1874) *Holbrookia elegans*; Cope (1880, 1883, 1894, 1895, 1896, 1900) *Holbrookia lacerata*, *Holbrookia maculata flavilenta*, *Uma scoparia*, *Uma inornata*, *Uma rufopuncatata*, *Callisaurus crinitus*, *Callisaurus rhodostictus*, *Holbrookia maculata maculata*, *Callisaurus draconoides ventralis*, and *Callisaurus ventralis gabbii*; Stejneger (1890) *Holbrookia maculata approximans* and *Holbrookia maculata lacerata*; Richardson (1915) *Callisaurus ventralis myurus*; Dikerson (1919) *Callisaurus carmenensis*; Schmidt (1921, 1922) *Holbrookia maculata campi*, *Holbrookia pulchra*, *Holbrookia dickersonae*, and *Callisaurus ventralis inusitatus*; Schmidt and Bogert (1947) *Uma exsul*; Barbour (1921) *Holbrookia thermophila*; Harper (1932) *Holbrookia propinqua stonei*; Smith (1935, 1943, 1946:137, 145) *Holbrookia elegans thermophila*, *Holbrookia elegans elegans*, *Holbrookia bunkeri*, *Holbrookia maculata ruthveni*, *Holbrookia maculata dickersonae*, *Holbrookia maculata pulchra*, and *Holbrookia maculata thermophila*; Linsdale (1940) *Callisaurus draconoides myurus* and *Callisaurus draconoides gabbii*; Heifetz (1941) *Uma notata notata*; Bogert and Dorsom (1942) *Callisaurus draconoides brevipes*; Smith and Burger (1950) *Holbrookia propinqua propinqua* and *Holbrookia propinqua piperata*; Peters (1951) *Holbrookia texana texana* and *Holbrookia texana scitula*; Axtell (1956) *Holbrookia lacerata*, *Holbrookia lacerata subcaudalis* and *Holbrookia maculata perspicua*; Smith and Cochran (1956) *Callisaurus draconoides rhodostictus*; and Williams, et al. (1959) *Uma paraphygus*.

Some summaries, reviews, checklists, and comparative studies have also been written. Cope (1896) synonymized *Uma* and *Callisaurus* in a short paper discussing the genus *Callisaurus*. He recognized *Uma* again in his large work on the crocodilians, lizards, and snakes of North America (1900) and recognized one species and three subspecies of *Callisaurus*.

Smith (1946:137, 145), in his "Handbook of Lizards," recognized in *Callisaurus* one species and ten subspecies and stated (p. 145): "The whole group of *Callisaurus* of western United States is in need of revision. The subspecies are not adequately characterized, nor are their ranges well worked out. There is very little information on the life history." Although we now know much more about the life history of *Callisaurus*, it is still in need of a comprehensive taxonomic review and remains a monotypic genus. (A careful revision for *Callisaurus* has not yet been attempted.)

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The genus *Holbrookia* has had two revisions. Schmidt (1922) made the first; a second was by Axtell (1958). Schmidt (p. 709) stated: "The taxonomy of the North American lizards of the genus *Holbrookia* Girard offers one of the most interesting and difficult problems in North American herpetology."

He recognized several species and states that (p. 712) "*Holbrookia* is obviously directly related to *Callisaurus*, from which it differs only in the concealed tympanum and with which it agrees in general features of color pattern and scutellation."

Smith (1946:137, 145) doubts that a practical means of characterizing the species exists and believes that "until such a means is found there will remain indefinitely a problem in defining the ranges of the several subspecies, or in defending their actual validity. Accordingly the genus, particularly the *maculata* group, merits a careful study perhaps more than any other in the United States."

Axtell (1958) recognized only three species, *Holbrookia lacerata*, *H. propinqua*, and *H. maculata*. He considered *H. texana* to be a species of the genus *Callisaurus* and therefore did not discuss it. He did list two subspecies for *lacerata*, two for *propinqua*, and 11 for *maculata*.

Uma has been reviewed by Heifetz (1941), Norris (1958), and Mayhew (1964b). Heifetz recognized *U. notata notata*, *U. notata cowlesi*, *U. inornata*, and *U. scoparia*. He also referred to the taxonomic confusion that exists because of erroneous type localities in this genus. In his checklist Schmidt (1953) recognized only one species (*notata*), with three subspecies (*notata*, *inornata*, and *scoparia*).

Norris (1958) recognized *Uma n. notata*, *U. n. rufopunctata*, *U. n. inornata*, *U. scoparia*, and *U. exsul*. He discussed the evolution of *Uma* and its relationship to other sand lizards.

The conflict relative to the classification of the *notata-scoparia* group was discussed by Mayhew (1964b). He recognized *U. inornata*, *U. notata*, and *U. scoparia* all as full species on the basis of temperature tolerance and reproductive data.

Peters (1951) reviewed *Holbrookia texana* (*Cophosaurus texanus*). He described two subspecies, but mentions little concerning relationships with other sand lizards.

Clarke (1965) revived *Cophosaurus texanus* on the basis of behavioral data collected in a large comparative study of the sand lizard group.

Ecological and behavioral studies concerning sand lizards have also been published by Burt (1931a, 1931b), Stebbins (1944, 1954, 1966), Ramsey (1948, 1949), Cagle (1950), Williams and Smith (1958), Axtell (1960), Lannom (1962), Carpenter (1963, 1967), Clarke (1965), Mayhew (1964a, 1964b, 1966), Pianka and Parker (1972), Tanner and Krogh (1975), and Judd (1974, 1975).

The anatomy of these lizards has not been thoroughly studied. Earle, in a series of articles (1961a, 1961b, 1961c, 1962), described in detail the comparative anatomy of the middle ear of sand lizards. Stebbins (1943, 1944) described the nasal structures and some aspects of the ecology of *Uma*, then (1948) described the nasal structures of lizards in general, which included the sand lizards. Axtell (1958) described the osteology of *Holbrookia* and stated that it is essentially the same as found in all sand lizards. Ethridge (1964) studied the skeletal morphology of sceloporine lizards, which includes sand lizards, and compared their relationships. Savage (1958) studied *Urosaurus* and *Uta* and made remarks concerning related genera, which included sand lizards. A few references to sand lizards were made by Larsen and Tanner (1974) while studying *Sceloporus*, and Guttman (1970b) also refers to them in his electrophoretic study of the hemoglobins of sand lizards. He found that all genera possessed the same major and minor protein components.

Only portions of the osteology have been adequately treated; the myology is essentially untouched. The objectives of this study are to: (1) describe the skull osteology and branchiomeric myology of sand lizards; (2) identify osteological and myological characteristics that distinguish the sand lizard generic groups; and (3) determine more accurately the relationships between these groups. No attempt will be made to deal with the species and subspecies except as they relate to the generic phylogeny.

Materials and Methods

Specimens used were obtained from the Brigham Young University Life Sciences Museum (BYU), the California Academy of Sciences (CAS), and the Strecker Museum at Baylor University. At least four specimens from each of the four genera were used for osteological examinations. The myology of these 16 specimens, plus four additional individuals from each genus, were also used in developing the myological description. The following list indicates the material used: *Callisaurus draconoides gabbi* from N.T.S., Nye Co., Nevada: (BYU) 2943, 2967, 3079, 40037; *C. d. inusatatus* from Tiburon Island, Sonora, Mexico: (BYU) 30175, 30176, 30178; *C. d. splendidus* from Isla Angel de la Guardia, Gulf of California, Mexico: (BYU) 41112; *C. d. carmenesis* from Baja California Sur, Mexico: (BYU) 41095, 41231; *Cophosaurus texanus texanus* from Chihuahua, Mexico: (BYU) 14339, 15712; *C. t. scitula* from Sierra Co., New Mexico: (BYU) 30512, 30513, 30515; *C. t. scitula* from Pima Co., Arizona: (BYU) 34331, 34336; *Holbrookia lacerata* from Giaraz Co., Texas: (CAS) 73979; *H. maculata approximans* from Colonia Dublan, Mexico: (BYU) 11370, 17099; *H. maculata bunkeri* from Chihuahua, Mexico: (BYU) 15782, 15785, 15788, 15789; *H. propinqua propinqua* from Padre Island, Cameron Co., Texas: (CAS) 16187; *Uma notata inornata* from Riverside Co., California: (BYU) 3263, 3266, (CAS) 22824, 22826; *U. n. cowlesi* from Sonora, Mexico: (BYU) 30144, 30156; *U. scoparia* from San Bernardino Co., California: (BYU) 11389, (CAS) 42072.

Skeletal material was prepared by careful dissection. Bones were cleaned with forceps and dissecting needles and soaked in Clorox bleach for several minutes to loosen soft tissues, after which further picking and cleaning was done. Skulls were not allowed to dry, but were preserved in 70 percent EtOH to insure that cartilaginous skeletal elements could be examined.

The Statistical Package for the Social Sciences (SPSS) discriminant analysis was utilized to aid in the identification of characters where they were not already obvious. The statistical analysis will be described below.

Myological examinations consisted of careful dissection in which each muscle was separated and its origin and insertion determined. General morphology (shape, relative size, and position) of each muscle was also noted. Muscle comparisons are based on both origin-insertion and muscle morphology. Only the branchiomeric muscles associated with the hyoid arch and the jaws are described.

Osteology

Sand lizard skulls have been examined in detail. The length and width of individual elements were measured with a Golgau vernier caliper and a five-millimeter mini-tool. Comparisons were made on the basis of ratios, as well as on the shape and position of each bone in relation to other articulating bones. The lower jaw and hyoid have been studied in the same manner.

The skull is streptostylic, with a freely movable quadrate bone. In mature individuals the ethmoid region of the braincase proper is not ossified, but consists of cartilage plates from which cartilaginous rods extend dorsad to add to and support the membranes that protect the brain. Eyes are large, and only a thin sheet of cartilage separates them medially; there is no apparent area of ossification, even in mature individuals.

The sand lizard skull follows the basic plan of Sceloporine lizards as described by

Ethridge (1964) and Larsen and Tanner (1974, 1975); there is a great deal of uniformity within the sand lizard group. We will not give detailed descriptions of each bone here; however, these data are available to those who may desire them. We will, however, describe the variations from the Sceloporine skull as well as the differences between the sand lizard genera.

The following is a list of the skeletal elements measured and described (they are illustrated on Figs. 1, 2, 3, 4):

Basioccipital
Supraoccipital
Vomer
Maxilla
Frontal
Parietal wing
Quadrate
Surangular
Coronoid
Orbit
Supratemporal fossa
Basisphenoid
Pterygoid
Palatine
Nasal
Infraorbital fossa
Jugal
Postorbital
Dentary
Splenial
Hyoid
Posttemporal fossa
Exoccipital
Ectopterygoid
Premaxilla
Prefrontal
Parietal
Squamosal
Articular
Angular
Temporal fossa

The sand lizard skulls differ from the general sceloporine skull in that they lack the lacrimal and the postfrontal bones. They differ among themselves in several ways, but most of the variance seems to be associated with the posterolateral position of the skull. The discriminant analysis selected 116 ratios that could aid in discriminating the four genera. Six measurements were found to be important. Every ratio selected included at least one of these six. They are listed along with their frequency of use: squamosal width (26), quadrate length (26), mandible length (20), hyoid length (20), mandible width (19), and maxillary length (15).

Representative ratio comparisons are given to illustrate the separation and relationships of genera. Figures (1-4) of the lateral, dorsal, and ventral aspects of the skull are also presented, including the lateral and medial views of the lower jaw and the dorsal view of the hyoid.

Earl (1961a, 1961b, 1961c, and 1962) reported on the osteological variations in the ear and indicated that all four groups were distinct, with *Cophosaurus* midway between *Callisaurus* and *Holbrookia.*

One of the first variations noticed, as skulls were being prepared, was that *Cophosaurus* and *Holbrookia* had a para-occipital process directed anterolaterally. That of *Callisaurus* and *Uma* is directed lateral or slightly posterior. As a result of this variation, variations in the length and width of the quadrate, squamosal, jugal, and postorbital were noted. In *Uma* and *Callisaurus* the ventral articulating process is ventral to the basioccipital, whereas in *Cophosaurus* and *Holbrookia* the quadrate is much shorter. *Uma* and *Callisaurus* also have a wider squamosal, and the squamosal and jugal just meet. In the earless genera the jugal pushes in between the squamosal and postorbital. In one *Uma* individual the squamosal and jugal failed to meet, and the postorbital had pushed in between them. Some other variations (such as the configuration of sutures between the frontal and parietal, the frontal and nasals, the basisphenoid and basioccipital, and the maxilla and premaxilla, as well as proportional variations in the maxilla, postorbital, and premaxilla) were also found, but they were slight and had no significance. These are attributed to individual variation on the species or subspecies level.

Myology

The myology of the neck and throat region has been carefully studied. Axtell (1958) pointed out that the intermandibularis muscle in the most anterior region of the throat is degenerate. The genioglossus is therefore the most ventral muscle in that region. This condition is constant throughout the sand lizard genera. The variations within the sand lizard genera are found in the intermandibularis muscles, depressor mandibularis, constrictor colli, and the omohyoideus-sternohyoideus complex.

The *intermandibularis anterior superficialis* (Figs. 5, 6) is a small muscle. In *Uma,* it is distinctly fan shaped. In *Callisaurus* and *Holbrookia* it is not fan shaped, and *Cophosaurus* shows a slight amount of fanning. In *Holbrookia* the fibers of this

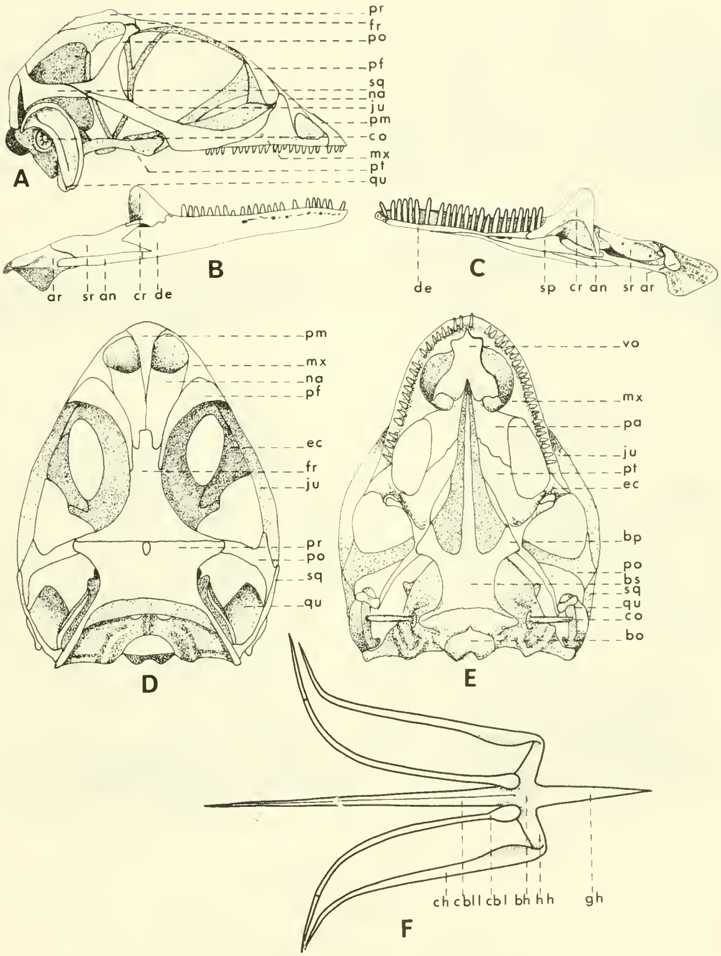
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Fig. I. The skull osteology of *Callisaurus* BYU 3079: A. lateral view of skull; B. lateral view of lower jaw; C. medial view of lower jaw; D. dorsal view of skull; E. ventral view of skull; F. dorsal view of hyoid. The symbols used are:

an–angular
ar–articular
bh–basihyal
bo–basioccipital
bp–basipterygoid
bs–basisphenoid
cbI–ceratobronchial I
cbII–ceratobronchial II
ch–ceratohyal
co–columella
cr–coronoid
de–dentary
ec–ectoptorygoid
fr–frontal
gh–glossohyal
hh–hypohyal
ju–jugal
mx–maxilla
na–nasal
pa–palatine
pf–prefrontal
pm–premaxilla
po–post orbital
pr–parietal
pt–pterygoid
qu–quadrate
sp–splenial
sq–squamosal
sr–surangular
vo–vomer

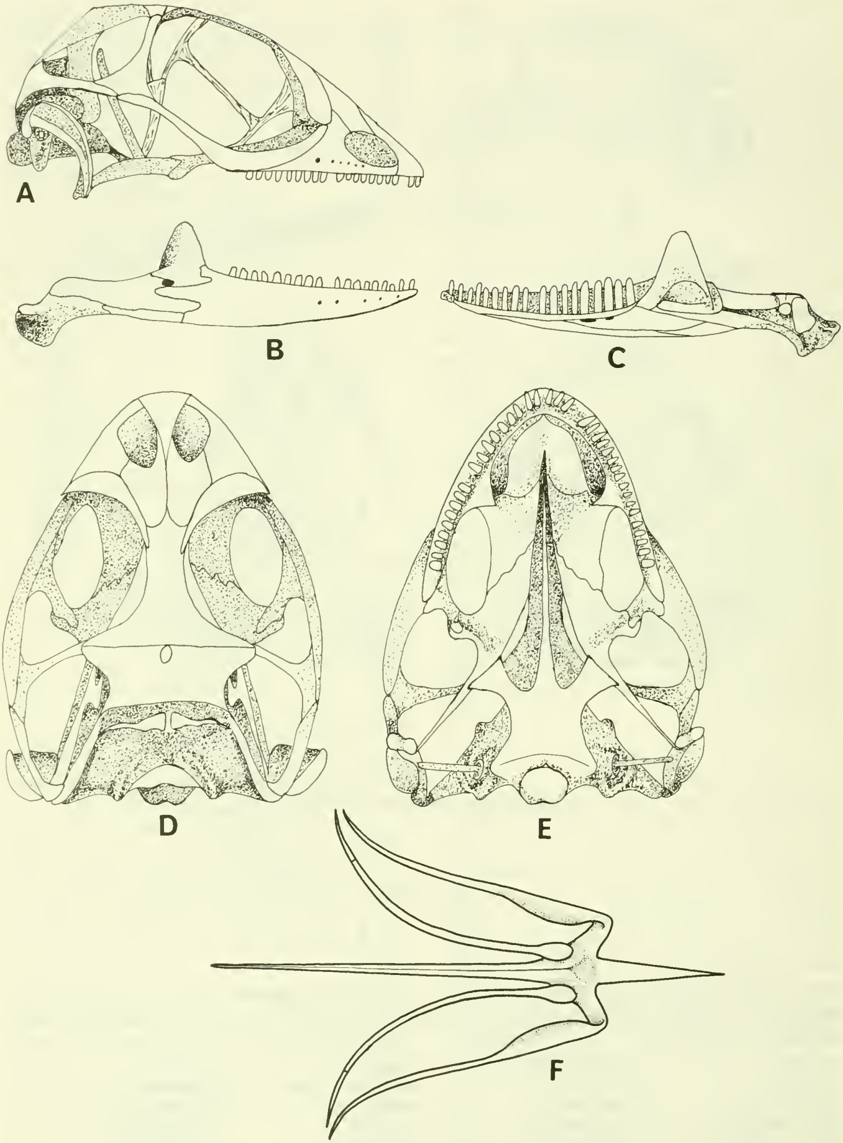

Fig. 2. The skull osteology of *Uma* BYU 3266: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

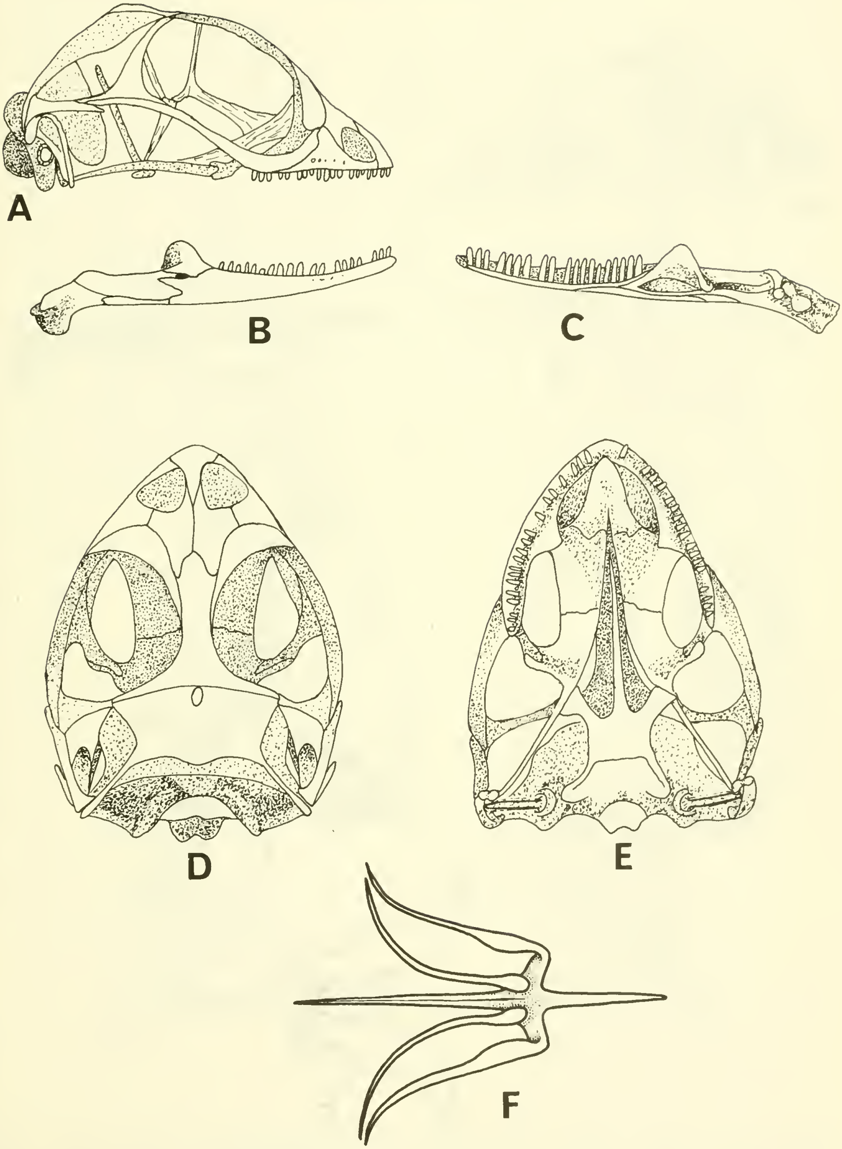

Fig. 3. The skull osteology of *Holbrookia* BYU 15783: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

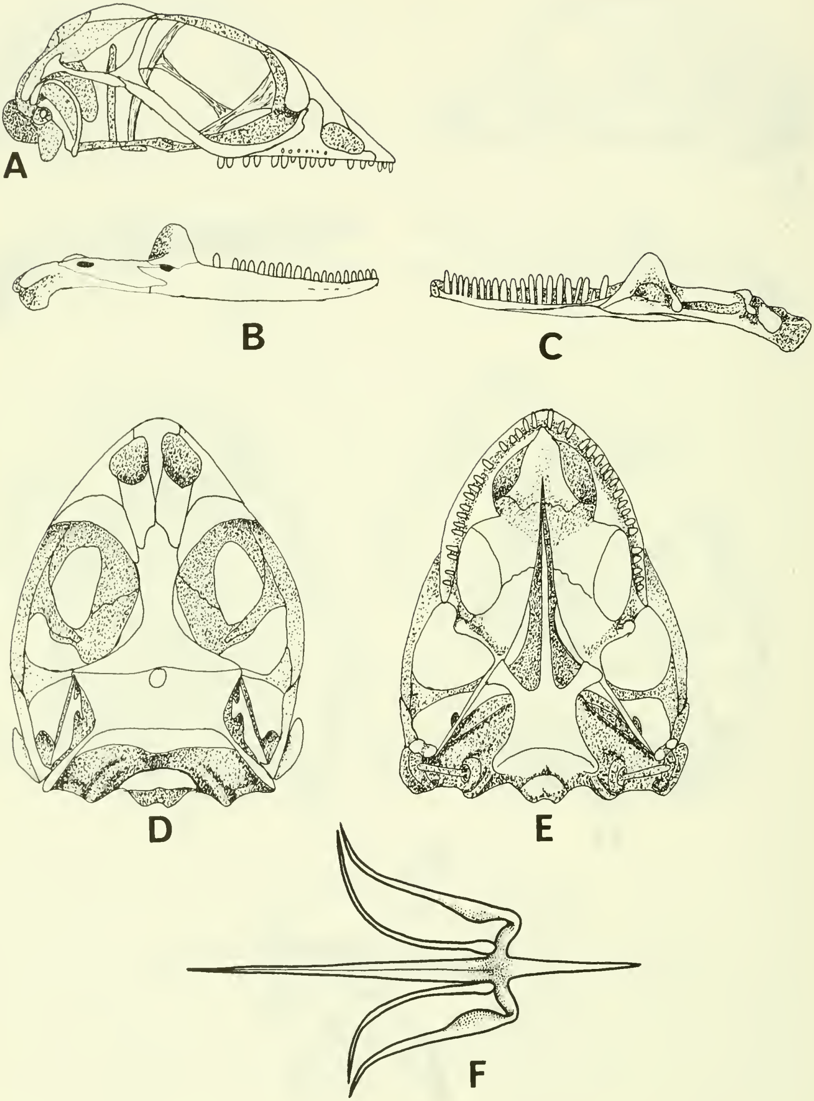

Fig. 4. The skull osteology of *Cophosaurus* BYU 30518: A; B; C; D; E; F; same as Fig. 1. The symbols used are the same as Fig. 1.

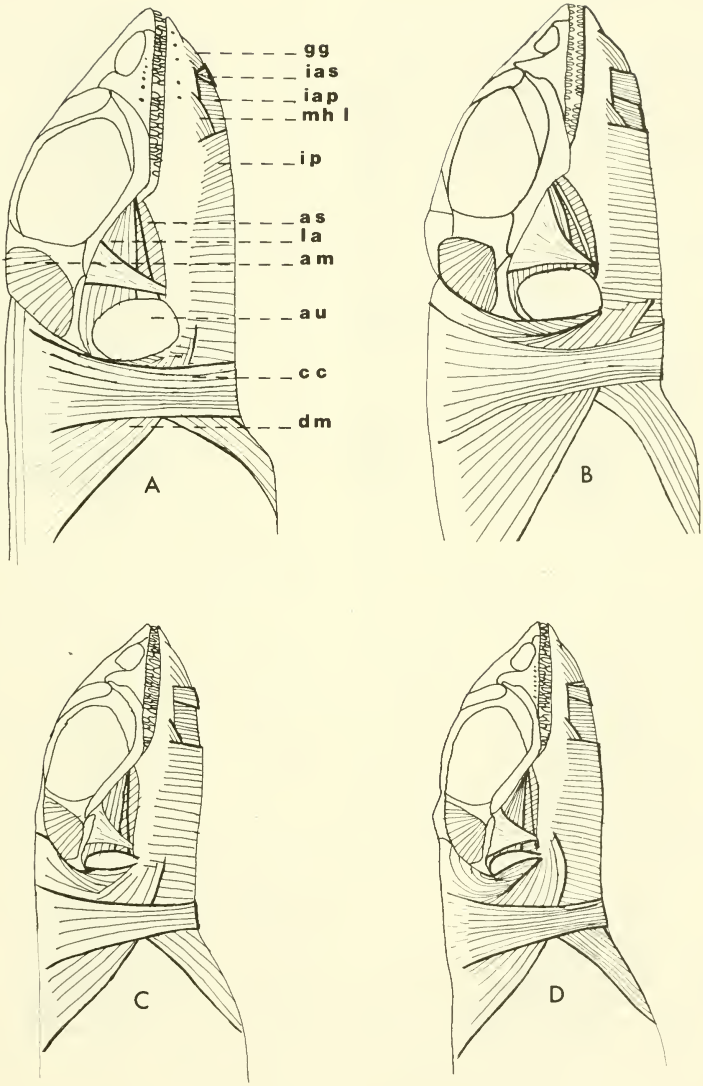

Fig. 5. Lateral view of head and neck musculature; superficial depth. A. *Uma* BYU 3263; B. *Callisaurus* BYU 2943; C. *Holbrookia* BYU 15782; D. *Cophosaurus* BYU 30512. The symbols used are: am–adductor mandibularis externus medius; as–adductor mandibularis externus superficialis; au–auditory meatus; cc–constrictor colli; dm–depressor mandibularis; gg–genioglossus; iap–intermandibularis anterior profundus; ias–intermandibularis anterior superficialis; ip–intermandibularis posterior; la–levator angularis oris; mhI–mandibulohyoideus I.

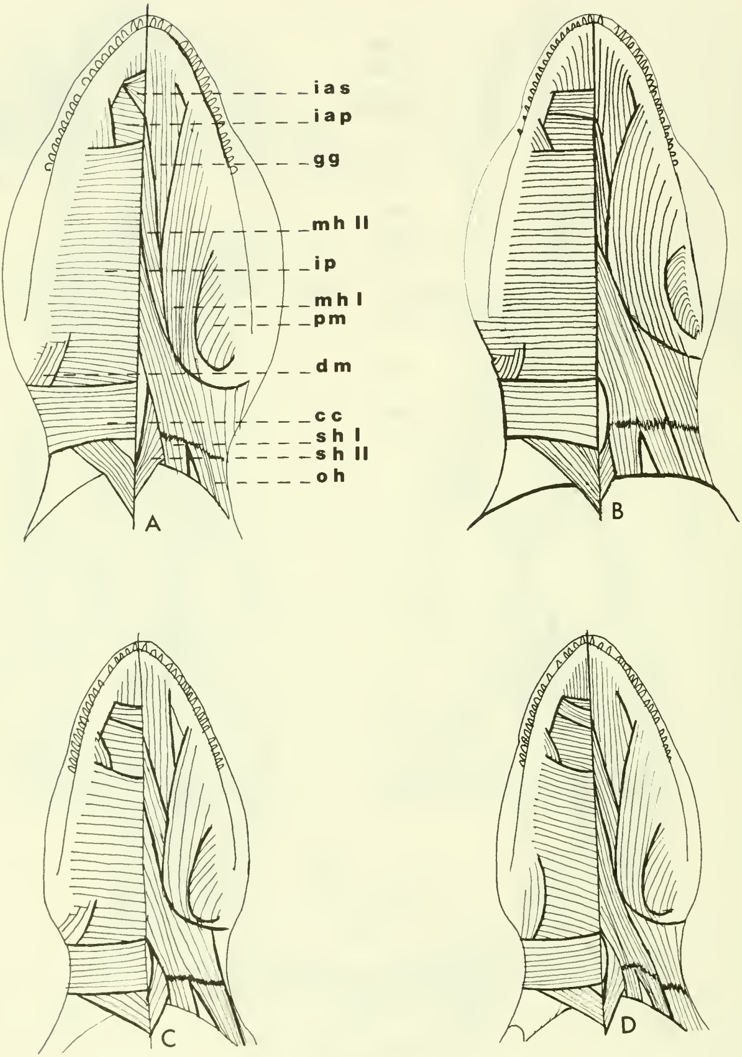

Fig. 6. Ventral view of throat musculature; superficial layer at left and first depth at right. A. *Uma* BYU 3263; B. *Callisaurus* BYU 2943; C. *Holbrookia* BYU 15782; D. *Cophosaurus* BYU 30512. The symbols used are: cc–constrictor colli; dm–depressor mandibularis; gg–genioglossus; iap–intermandibularis anterior profundus; ias–intermandibularis anterior superficialis; ip–intermandibularis posterior; mhI–mandibulohyoideus I; mhII–mandibulohyoideus II; oh–omohyoideus; pm–pterygomandibularis; shI–sternohyoideus I; shII–sternohyoideus II.

muscle pass posteromedial, whereas in the other three genera they pass transversely or fan out.

The *intermandibularis anterior profundus* (Figs. 5, 6) occupies a position posterior and dorsal to the intermandibularis anterior superficialis, and anterior and dorsal to the intermandibularis posterior. In *Uma* the fibers extend medially, with only a few fibers at each end fanning out. In *Cophosaurus* it is distinctly fan shaped, and in *Callisaurus* it fans out to a lesser degree. In *Holbrookia* it is slightly fan shaped, with most fibers slanting posteriorly. There were two areas of variation seen in the neck musculature.

The *constrictor colli* (Figs. 5, 6) is the superficial muscle of the neck, originating in the dorsolateral fascia of the neck and inserting in the ventral raphe of the throat posterior to the intermandibularis posterior. It is one or two muscle fibers thick, rather narrow, and the origin is broader than the insertion.

In all four genera the muscle fibers of the constrictor colli reach the mid-throat area, but they originate in a facia without reaching the dorsal skeletoginous septum.

The constrictor colli is widest in *Uma*. It covers from the posterior edge of the tympanum to the shoulder, nearly covering the depressor mandibularis completely. In the other three genera it is more straplike and only fills half the space between the posterior edge of the tympanum and shoulder, being centered in this area.

The *depressor mandibularis* (Figs. 5, 6) originates in the mid-dorsal raphe, along the posterior borders of the parietal bone and parietal wings. The insertion has three slips; one inserts deep to the pterygomandibularis on the articular process of the lower jaw. Another passes superficially to the pterygomandibularis and the intermandibularis posterior; it inserts on the ventrolateral surface of the mandibular rami by interdigitating at right angles with these muscles. The third slip inserts on both sides of a tendon that extends dorsally from the articular process. The attachment of this slip to the articular is superficial to the deep slip mentioned above. In the earless lizards (*Cophosaurus* and *Holbrookia*) a portion of this muscle is expanded anteriorly to partially cover the tympanic cavity.

The *sternohyoideus* I and omohyoideus are closely related, and there is considerable confusion in the literature concerning them. The position taken here is that those portions that originate on the scapula and clavicle are omohyoideus, and those portions that originate on the sternum are sternohyoideus.

Both muscles are deep to the constrictor colli, and the episterno-cleidomastoideus. The muscle dorsal to them is the sternohyoideus II.

The *omohyoideus* (Fig. 6) takes two forms; in *Uma* and most species of *Holbrookia* it has a single head originating on the scapula and clavicle. In *Callisaurus*, *Cophosaurus*, and some *Holbrookia* the omohyoideus is divided for its entire length, connected only by a myocomma located midway between the origin and insertion, bisecting the muscle and binding the muscle fibers together. This myocomma also bisects the sternohyoideus I, and the two muscles are bound firmly together by it.

The omohyoideus can be easily separated from the sternohyoideus posterior to the myocomma, but they cannot be distinguished anterior to it except by position.

The *sternohyoideus I* (Fig. 6) originates on the sternum and inserts on the proximal end of the ceratobranchial I and II. The myocomma is at its junction with the omohyoideus, and it unites the two muscles. The medial portion of the omohyoideus cannot be distinguished from the sternohyoideus anterior to this myocomma in all genera.

Statistical Analysis

The osteology of the skulls was analyzed by taking 43 measurements from each skull and by calculating all possible ratios. The Statistical Package for the Social Sciences (SPSS) discriminant analysis was employed to determine which ratios were of value in distinguishing genera and if the lizards could be classified by using them. The theory and use of discriminant analysis is described by Klecka (1975). From each skull 903 ratios were generated, and those sufficient to separate one genus from the other three were used.

The discriminant analysis proceeds in a stepwise fashion by selecting the single best-discriminating variable, and then selects a second on the basis of its ability to improve the value of the discrimination criterion in combination with the first variable. Third and subsequent variables are similarly selected according to their ability to contribute to further discrimination. A plot of the discriminant score in two dimensions, a territorial map, and a classification based on the preceding analysis are given. Range, mean, and standard deviation of ratios for each genus are also given, and examples are presented in Figs. 7 and 8 along with a plot of the ratios (Figs. 7–11) that illustrates relative relationships between genera. These figures are only examples of the ratios, and were selected because they clearly demonstrate the results referred to below.

A multivariate analysis of variance was performed to determine the significance of differences between the four genera. The comparisons were based on a non-orthoganal set such that the differences between *Uma* and the other three genera were tested (comparison #1), the differences between *Callisaurus* and *Cophosaurus* were tested (comparison #2), and, finally, the differences between *Cophosaurus* and *Holbrookia* were tested (comparison #3).

Using 116 ratios selected in the discriminant analysis, it is possible to classify the four genera. Of 21 tests, classification agreed with the present taxonomic system in 17 of them. The first classification error was in Test 7, where a *Callisaurus* and a *Cophosaurus* were both classified as *Holbrookia*. Only three ratios were involved, and all three involved the squamosal width divided by the vomer width, palatine length, and palatine width respectively. These ratios were effective in separating *Uma* from the other three, but were not useful in distinguishing between the other three genera.

The second classification error occurred in Test 8. Here a *Callisaurus* and a *Holbrookia* were both classified as *Cophosaurus*. Four ratios were involved, and each one used the squamosal width divided by the pterygoid width, the epipterygoid width, the hyoid length, and the hyoid width. Whereas *Uma* was well separated in Test 7, it was not well separated in Test 8.

The most confused classification was in Test 15. Here one *Callisaurus* and one *Holbrookia* were both classified as *Cophosaurus*, one *Callisaurus* was classified as *Uma*, one *Cophosaurus* was classified as *Holbrookia*, and one *Holbrookia* was classified as *Callisaurus*. Two ratios were used, and they were derived from the mandible width divided by the frontal width and the nasal width. *Uma* is the most distinct in this test; however, the individual plot scores show

Genus	Range	Mean	Standard Deviation
Callisaurus	9.6875 to 12.3636	10.8422	1.1974
Cophosaurus	10.3333 to 13.8889	11.7222	1.5437
Holbrookia	11.5000 to 13.7500	12.1583	1.1751
Uma	5.4375 to 7.1379	6.1048	0.7827
Total	5.4375 to 13.8889	10.2069	2.7175

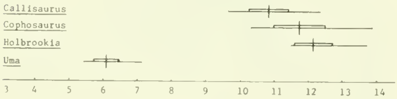

Fig. 7. Ratio of the skull length/squamosal width used in Test #5 of the Discriminant Analysis. Range, mean, and standard deviation plotted for the ratio of skull length/squamosal width in the four current genera.

Genus	Range	Mean	Standard Deviation
Callisaurus	4.5405 to 5.6667	5.0379	0.4923
Cophosaurus	5.2963 to 5.6000	5.4190	0.1337
Holbrookia	4.7500 to 6.7647	5.5560	0.9255
Uma	4.0200 to 4.3500	4.1624	0.1373
Total	4.0200 to 6.7647	5.0438	0.7361

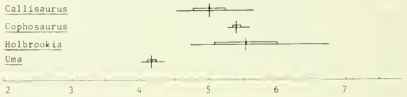

Fig. 8. Ratio of the skull length/mandible width used in Test #14 of the Discriminant Analysis. Range, mean, and standard deviation plotted for the ratio of skull length/mandible width in the four current genera.

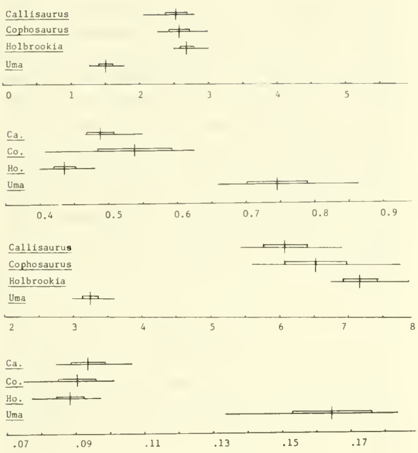

Fig. 9. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. squamosal length/squamosal width; B. squamosal width/quadrate length; C. jugal length/squamosal width; D. squamosal width/mandible length.

considerable variation, and there is no discrete grouping to distinguish the separate genera.

The last confused classification was in Test 17. Here four ratios were used that involved the mandible width divided by the palatine length, palatine width, epipterygoid length, and the mandible length. In this classification a *Callisaurus* and *Cophosaurus* were both mistaken for *Holbrookia*. The plot indicates a complete separation of *Uma*, but with an overlap of the other three genera.

Over all 21 tests the centroids were separated on the average of the following distances: *Uma* was separated from *Callisaurus* by 2.10 mm, from *Cophosaurus* by 2.44 mm, and from *Holbrookia* by 2.67 mm; *Callisaurus* was separated from *Cophosaurus* by 1.19 mm and from *Holbrookia* by 1.58 mm; and *Cophosaurus* was separated from *Holbrookia* by 0.92 mm. These centroids are derived from the discriminant functions, which in turn are derived from linear combinations of the variables used in each test. The purpose for the discriminant analysis was to find ratios that would discriminate

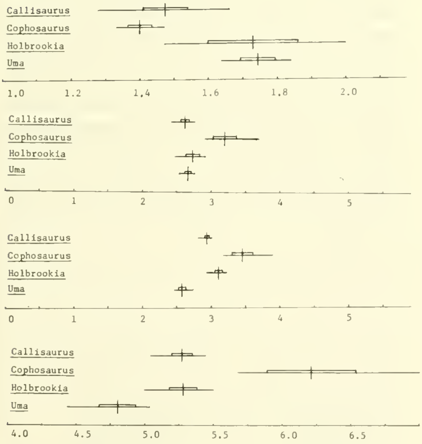

Fig. 10. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. quadrate length/quadrate width; B. maxillary length/quadrate length; C. jugal length/quadrate length; D. skull length/quadrate length.

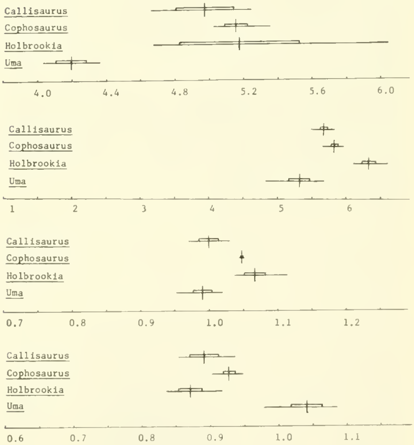

Fig. 11. Range, mean, and standard deviation in the four current genera plotted for the ratios of: A. mandible length/mandible width; B. jugal length/mandible length; C. skull length/jugal length.

between the groups; this goal was achieved. It is also desirable to determine how well each group is defined, and if it is significantly different from all other groups. The SPSS program does not provide this information, but it is possible, by studying the plots (Figs. 7–11), to see that the range of *Callisaurus* overlaps the range of *Holbrookia* and/or *Cophosaurus* in nearly all ratios plotted. The range for *Uma* is only occasionally overlapped by the other genera, and it is usually only *Callisaurus* that overlaps *Uma*.

The multivariate analysis of variance was performed to determine the degree of significance between the four genera. The nonorthoganal set of comparisons was as follows:

Comp.	*Cal.*	*Coph.*	*Hol.*	*Uma*
1	1	1	1	–3
2	–1	1	0	0
3	0	1	–1	0

The degrees of freedom, F-ratios, and actual probability for each F-value are presented in Table 1.

The differences between *Uma* and the other three genera are highly significant, but the differences between the remaining three genera are only slightly significant, and in many cases the differences are insignificant.

Uma is therefore the best differentiated by these tests. The other three genera are close together, and although they can be distinguished on the computer, their degree of separation is slight.

The probability of error in differentiating between *Callisaurus* and *Cophosaurus* is similar to the probability of error in differentiating between *Cophosaurus* and *Holbrookia* (average between 9 percent and 12 percent), verifying these statements.

These data are based on 116 ratios that were found to be the best discriminators of the 903 ratios examined. It is noteworthy that by using the very best osteological discriminators, the genera are often not clearly separated.

DISCUSSION

Sand lizards are a closely related group according to Smith (1946), Norris (1958), Axtell (1958), Etheridge (1964), and Clarke (1965). Smith referred to them as a closely knit group and listed their common characteristics as being oblique labials, granular dorsal scales, small head scales, a gular fold, a peculiar median triangular postmental, several prominent postlabials, much the same habits, similar habitat, scoop-shaped heads, flaring labial regions, and a countersunk lower jaw. Axtell (1958) listed 22 characters that he felt would describe ancestral sand lizards. With only a few exceptions, this list of characters might just as well apply to other sceloporine lizards.

Callisaurus, *Cophosaurus*, and *Holbrookia* exhibit many of the primitive characteristics mentioned by Axtell. Each genus, however, shows specializations that vary from those listed. *Callisaurus* is similar to Axtell's cri-

TABLE 1. Summary of F-ratios from eight multivariate analyses of variance tests.

		Comparisons		
		1	2	3
Test	df.	F-ratio/Probability	F-ratio/Probability	F-ratio/Probability
1	6/7	7.797/0.79%	1.858/21.8%	4.034/4.51%
2	7/6	11.055/0.468%	4.623/4.05%	1.973/21.29%
3	7/6	25.922/0.044%	4.596/4.106%	31.230/0.026%
4	5/8	96.377/0.000062%	1.141/41.24%	2.827/9.25%
5	6/7	12.387/0.20%	16.830/0.077%	4.450/3.56%
6	5/8	40.174/0.00185%	2.100/16.76%	6.117/2.54%
7	6/7	10.251/0.35%	14.480/0.124%	2.147/17.02%
8	4/9	7.807/0.532%	4.670/2.572%	2.118/16.07%

teria for the primitive condition, with the most striking specializations being increased length of tail and limbs and a more slender body form. *Holbrookia* is also similar to ancestral sand lizards except for the covered tympanum. Body form in *Holbrookia* is not as proportionately slender as it is in *Callisaurus*, nor is the tail as long. The problematic *Cophosaurus* has characteristics of both. Its body form, limbs, and tail approach those of *Callisaurus*, but it has a covered tympanum like *Holbrookia*. *Uma* has developed, to a greater degree, the dorsoventrally flattened body and the toe fringes. *Callisaurus*, *Holbrookia*, and *Cophosaurus* occupy generalized habitats, probably similar to that of the ancestral stock. *Uma*, on the other hand, is restricted to a sand dune habitat.

Osteology

Comparisons of skulls of *Ctenosaura* (Oelrich 1956), as well as general accounts of reptile osteology by Williston (1925), Romer (1956), and Avery and Tanner (1964, 1971) indicated that osteological characteristics of iguanid lizard skulls are generally stable within a genus. Studies on *Sauromalus* (Avery and Tanner 1964), *Crotophytus* (Robison and Tanner 1962), and *Ctenosaura* (Oelrich 1956) portrayed the apparent general stability of osteological characters found in iguanid skulls; however, skulls of *Callisaurus, Cophosaurus, Holbrookia*, and *Uma* observed in this study are peculiar to iguanid skulls as portrayed by the above authors because there is stability within the sand lizard genera as a group rather than within a single genus. The lacrimals and postfrontals are also absent in all the sand lizards, a condition not generally found in iguanid skulls, except that Jenkins and Tanner (1968) found that two species groups of *phrynosoma* also lack these skull bones. Etheridge (1964) pointed out the absence of the lacrimals and postfrontals in sand lizards.

Deviation by sand lizards from the general iguanid skull, particularly evidenced by the fusion or loss of the lacrimal and postfrontal bones, is evidence supporting the hypothesis that sand lizards are highly specialized among the iguanids.

In discussing the osteology of *Holbrookia*, Axtell (1958:24) stated:

> In general the osteology of the genera *Callisaurus* and *Uma* corresponds closely with that of *Holbrookia*, so this discourse may apply just as well to the entire sand lizard section of the family iguanidae.

Development of the covered tympanum appears to be related to the osteological variations observed in this study. The quadrate, squamosal, paraoccipital process, and mandible are all adjacent to the ear, and all exhibit variations (Figs. 1, 2, 3, and 4). With the loss of the external ear, the quadrate is reduced in size, and the paraoccipital process is directed forward, the mandible is shortened, the squamosal is narrowed, and the hyoid is also shortened. These modifications of the skull are apparent in earless sand lizards and are less modified in sand lizards having an external ear. *Callisaurus* and *Uma* are alike in that the paraoccipital process is directed caudad, the quadrate proportionately larger, and the mandible long and wide in comparison to the earless forms (Figs. 1, 2, 3, and 4). In *Uma* the degree of development of these characters is different because the squamosal is wide. A ratio of skull length divided by squamosal width shows: (a) *Uma* ranging from 5.4375 to 7.1379; (b) *Callisaurus* ranging from 9.6975 to 12.3636; (c) *Cophosaurus* ranging from 10.3333 to 13.8889; and (d) *Holbrookia* ranging from 11.0833 to 13.7500 (from Fig. 7). The quadrate and mandible length and width are similarly enlarged in *Uma* when compared to the other groups. These differences are sufficient to permit the computer to distinguish between these measurements in *Uma* and those same characteristics found in *Callisaurus* and the earless group.

There is some variation in the position and articulation between the squamosal, jugal, and postorbital. In all except some *Uma* individuals, the jugal reaches the squamosal. In *Callisaurus* it edges between the squamosal and postorbital. In *Holbrookia* and *Cophosaurus* the degree of encroachment is increased. This may be a result of the forward direction taken by the paraoccipital process and the shortening of the jaw. *Uma* is unique in that the jugal fails to reach the squamosal in some individuals, in which case the postorbital is found wedging between them (Fig. 3). In other *Uma* individuals a mere contact is made without any overlap of the squamosal and jugal.

That these variations exist is verified by the statistical analysis. The SPSS discriminant analysis was able to identify characteristics that were capable of separating the genera into distinct groups. However, the analysis of variance points out that differences between *Callisaurus*, *Cophosaurus*, and *Holbrookia* (as identified by SPSS) are insignificant and that *Uma* is indeed a distinct group. The F-ratios derived from the analysis of variance illustrate these facts. The tests comparing *Uma* with the other three genera have high F-values (96.377 to 7.797) and consequently low probability of making classification errors (from 0.000062 percent to 0.79 percent). Therefore the differences between *Uma* and the other sand lizards are highly significant. In comparing *Callisaurus* with *Cophosaurus*, the F-values were found to be lower (16.830 to 1.141), and consequently the probability of classification error is higher (41.24 percent to 0.077 percent). Only two of the eight tests were significant (below 2.5 percent probability of error). The tests comparing *Cophosaurus* with *Holbrookia* are similar to those comparing *Callisaurus* and *Cophosaurus*. The F-ratios range from 31.231 to 1.973. The probability of error is again higher (21.29 percent to 0.026 percent). Low F-ratios and high error probability indicate that the differences between the three genera are insignificant.

Myology

The literature is void of studies dealing directly with myology of sand lizards. Earle (1961a, 1961b, 1961c, 1962) dealt with the middle ear and also touched on the myology in the ear region. In this study, we will deal only with the myology of the head and neck region. A comparison of the anterior anatomy of sand lizards shows some observable differences that are discussed below (Figs. 5 and 6).

The intermandibularis muscles show some variations that are useful in distinguishing the genera. *Uma* is most distinct, with its intermandibularis anterior superficialis muscle being fan shaped (Fig. 6). This condition is contrasted with that found in *Holbrookia*, where the transverse mandibulae muscles are so nearly parallel that the borders of each muscle are difficult to discern. *Cophosaurus* and *Callisaurus* exhibit an intermediate condition with some fanning seen, but not to the extent seen in *Uma*. *Cophosaurus* can be distinguished from *Callisaurus* in that fibers of the intermandicularis anterior superficialis extend posteromedially, and in *Cophosaurus*, a portion of the insertion of the intermandibularis anterior profundus is found anterior to the superficialis, a condition not seen in *Callisaurus*.

The depressor mandibulae also shows some variations. In the earless lizards there is an expanded anterior edge of this muscle, which partially covers the enclosed tympanum. This muscle emerges from beneath the constrictor colli to insert upon the mandible, with its most ventral fibers interdigitating at right angles with the intermandibularis posterior. Furthermore, the depressor mandibulae fibers extend much further along the mandibular ramus than in the eared genera. In *Cophosaurus* these fibers reach the mandibular ramus with only a few interdigitating with the intermandibularis posterior.

The omohyoideus is also variable in these genera. In the unfolding of the evolutionary development of the omohyoideus, a branch of the rectus cervicus originated on the scapula and inserted on the hyoid. In sand lizards it further developed into a complex of muscles. In *Uma* the omohyoideus has a second head that originates on the sternum. This then can be called sternohyoideus I. Another muscle, the sternohyoideus II, arises on the sternum, passes deep to the sternohyoideus I, and inserts on the posterodorsal edge of the ceratobranchial I. Avery and Tanner (1964) designated this muscle thyrohyoideus in *Sauromalus*, but, since it clearly originated on the sternum in sand lizards, it is designated sternohyoideus II in this study.

A division of the omohyoideus has occurred in *Callisaurus*, *Cophosaurus*, and two specimens of *Holbrookia* (*Holbrookia lacerata* CAS 73979 and *Holbrookia m. approximans* BYU 17099). Thus, in sand lizards the muscle may have one to three origins: the most lateral dorsal one is on the scapula, the second is on the clavicle, and the most medial is on the sternum and interclavicle. The omohyoideus also has two insertions: the most lateral division inserts on the distal two-thirds of the ceratobranchial I, and the second and medial heads unite and insert on the proximal third of the ceratobranchial II and the basihyal. In *Uma* and for the most part in *Holbrookia*, such division of the omohyoideus has not occurred, and the insertion is continuous along the ceratobranchial I, the basihyal, and the proximal third of the ceratobranchial II. These myological variations, although observable, are not of great magnitude and may not be sufficient to support generic status for *Callisaurus*, *Cophosaurus*, or *Holbrookia*. In all there is an overwhelming myological similarity within these three genera, and they are obviously closely related to *Uma*.

Phylogeny

Norris (1958) and Axtell (1958) agreed that sand lizards began their radiation in early or middle Miocene. This is the time when the Sierra Madre Occidental Range of Mexico was being built by volcanism along the western and southern borders of the Mesa of Central Mexico (Schuchert 1935, Miller 1942). Axtell indicated that this volcanism split the sand lizards into two groups, a *Uma-Callisaurus* group and a *Holbrookia* prototype. Norris also believed the sand lizards were divided at this time, but indicated that *Uma* was isolated from the *Callisaurus-Holbrookia* stock. Norris further indicated that *Uma* was subsequently split by continued mountain-building processes in the mid-Pliocene, giving rise to the *exsul* group and *notata-scoparia* stocks. He also postulated that it was during this same time that the *Callisaurus-Holbrookia* stock was divided. The data available to us from this study tend to support Norris' concepts concerning the radiation of sand lizards. According to Maslin (1952), "The basic assumption upon which all taxonomic practices rest is that similar organisms are related." If we assume that sand lizards have occupied similar habitats and have been subject to similar environments throughout their recent history, then we can assume that the degree of similarity between groups is an indication of the closeness of their relationship. Maslin (1952) also states that because internal characters are less variable, they are of much greater value in establishing relationships than are external characters. The internal characters considered here indicate a closer relationship between *Holbrookia* and *Callisaurus* than between *Uma* and *Callisaurus*, indicating that *Uma* was probably the first of the sand lizards to break away from the ancestral line.

Clarke (1965) examined the behavior and external morphology from the standpoint of 20 characters; in 14 of them *Cophosaurus* was like *Callisaurus*, in 5 of them *Cophosaurus* was unique, and in only one was *Cophosaurus* like *Holbrookia*. In discussing these comparisons he states:

> The distinctness of *Cophosaurus* is evident. It is intermediate in many features between *Callisaurus* and *Holbrookia*, with the data indicating a closer affinity to *Callisaurus* than to *Holbrookia*. The uniqueness of *Cophosaurus* is most clearly shown in the distinctness of the push-up pattern.

On the basis of five characters, Clarke would separate *Cophosaurus* as a separate genus. These five characters are: (1) placement of the lateral bar: anterior for *Callisaurus*, posterior for *Cophosaurus*, and central for *Holbrookia*; (2) body shape: slender for *Callisaurus*, intermediate for *Cophosaurus*, and stout for *Holbrookia*; (3) middle ear: distinct with an external opening for *Callisaurus*, distinct without an external opening for *Holbrookia*, and intermediate without an external opening for *Cophosaurus*; (4) preferred body temperature: 39.2 C for *Callisaurus*, 38.3 C for

Cophosaurus, and 35.7–38.1 C for *Holbrookia*; and (5) push-up pattern: distinct in all three groups. In four of the five characters the differences are only comparative, and do not indicate a clear-cut distinction; only in the fifth does *Cophosaurus* show a real distinctness.

An alternate interpretation of these data would have to conclude that there is not enough difference to warrant generic status for *Cophosaurus*; indeed, there also may not be enough difference to warrant generic status for *Holbrookia*. The variations described are of the kind and magnitude used in the descriptions of species. Clarke (1965) stated that the push-up pattern is the most distinct feature of *Cophosaurus*. Carpenter (1963, 1967) described the same behavior for *Uma*, indicating that a genus is capable of supporting greater variation than Clarke has allowed for in *Callisaurus*, *Cophosaurus*, or *Holbrookia*.

Guttman (1970b) also commented on Clarke's study, stating:

> A comparison of *Callisaurus*, *Cophosaurus*, and *Holbrookia* (Clarke 1965) indicated the great similarity among these genera. According to Clarke, the uniqueness of *Cophosaurus* is most clearly shown by its distinctive push-up pattern. A comparison of the display-action patterns of two species of *Urosaurus* (Carpenter 1962) or three species of *Uma* (Carpenter 1963) indicated to this writer that sufficient intrageneric variation exists to refrain from establishing a genus based on this display pattern.

Guttman was reporting his electrophoretic study of sand lizards, in which he analyzed the hemoglobin components and found that they were all identical. This is highly unusual, especially for different genera. Electrophoretic techniques have been of value in confirming taxonomic relationships. This has been demonstrated by Dessaur et al. (1962), Dessauer (1966), Gorman and Dessauer (1965), Gorman (1966), Maldonado and Ortez (1966), and Guttman (1970a and 1970b). The conclusion Guttman (1970b) came to, and the one that supports our conclusions, was that the sand lizards are more closely related than their present taxonomic status indicates.

Simpson (1945) states:

> What is deplorable in splitting is the tendency to raise the ranks of groups without need, that is, without gaining any practical advantage. One of the more evident symptoms of this tendency is the appearance of many monotypic groups in classification.

The proposal resulting from this study and data examined from other studies would eliminate one monotypic genus and would provide a better indication of the close relationships that are so evident in the sand lizards.

Axtell (1958) believed that the sand lizards evolved under subhumid conditions, not greatly different than the conditions existing today in the sand lizard range. He postulates that it was during the mid-Pliocene that *Holbrookia* developed the covered tympanum. He then states, "The species previously known as *Holbrookia texana*, but which now appears to belong in the *Callisaurus* line of evolution, has probably developed the covered tympanum independently." Axtell's phylogenetic tree for the sand lizards is presented in Figure 12.

Earl (1961a, 1961b, 1961c, and 1962) indicated that *Cophosaurus* was intermediate between *Callisaurus* and *Holbrookia* in ear anatomy, but agreed with Axtell that earlessness evolved twice, reporting that re-

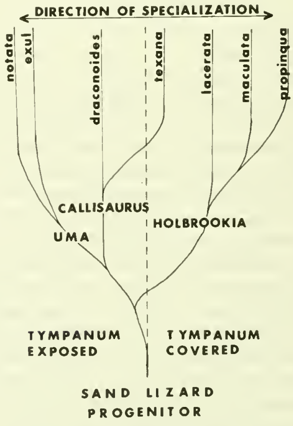

Fig. 12. Phylogeny of the sand lizards according to Axtell (1958).

lated groups have the potentiality to develop identical clines, and under similar environmental conditions these identical clines may develop at different times and places. This concept was discussed by Maslin (1952), who put forth the idea while discussing morphological criteria of phyletic relationships. Norris (1958) and Clarke (1965) also agreed with Axtell about the idea of separate earless evolution.

The concept of two evolutions for earlessness may be a major barrier to the understanding of sand lizard relationships. Since we lack a fossil record of sand lizards, there is no way of knowing when or how such a character came about. It has been suggested (Earl 1961a) that it came about in response to the burrowing habit, but this is purely speculative, as there are many burrowing species that do not have a covered tympanum (including *Uma*). A covered tympanum is not unique to "sand lizards" because the agamid genus *Tympanocryptis* in Australia is earless, and so are some of the members of *Phrynocephalus*. *Phrynosoma* has both eared and earless members. Norris's (1958) idea is acceptable when he says that *Callisaurus* and *Holbrookia* split in the early Pliocene, with *Holbrookia* occupying the table lands of the mesa of Central Mexico, and *Callisaurus* having been isolated from *Holbrookia* before their radiation to the more northern habitats. The habitats of the Chihuahuan desert and Sonoran desert are similar; the *draconoides* and *texanus* groups would have had an excellent opportunity to parallel each other sufficiently to account for the external morphologic similarities. Internal structures are not as accessible to external selective pressures and may, then, indicate more accurately the true relationships: that the *texanus* group is more closely related to *Holbrookia* than to *Callisaurus*, which it resembles through parallelism.

That earlessness may have evolved twice is possible, and it is most probable that there were separate evolutions for this character in the genera *Tympanocryptis*, *Phrynocephalus*, *Phrynosoma*, and sand lizards. To theorize that it evolved twice in the sand lizards is, however, a questionable concept. Earless sand lizards are closely related, their geographic ranges overlap, their habitats are similar, their food requirements are similar, the ear anatomy is similar, and we lack any evidence from fossil records that they diverged before the earless character arose. Where evidence indicates a close taxonomic relationship, as it does here, the idea of a single evolution for the earless character is most plausible. It is very unlikely that the same character would evolve twice in the same way in two groups that are as closely related as are earless sand lizards. (A proposed phylogenetic tree is given in Figure 13.)

These data, when added to that of earlier workers, seem to clearly indicate that sand lizards may best be represented by three genera: *Uma*, *Callisaurus* (as at present constituted), and *Holbrookia*.

The characteristics that separate sand lizards into genera are few and not well defined when compared to distinctions between other Sceloporine genera. The relationship between *Callisaurus* and *Holbrookia* is especially close, with earlessness (and its associated skull characters) and body proportions being the most striking variants. *Uma*, on the other hand, appears to be well defined. It is felt that *Holbrookia* is, therefore, a recent derivative of *Calli-*

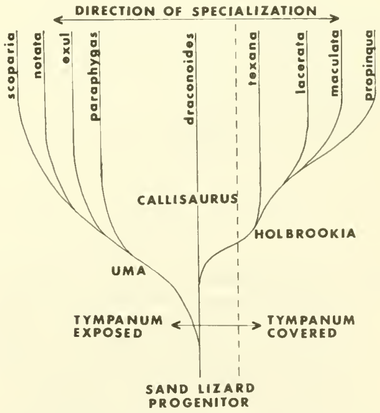

Fig. 13. Proposed phylogeny of the sand lizards as dictated by data developed from this study.

saurus, evolving earlessness and an adaptation for varied habitats in a relatively short time, perhaps since their separation in the late Pliocene.

Sand lizards, particularly the species and subspecies, particularly in *H. maculata*, indicate that this group has recently undergone adaptive radiation. If recent geological past has been correctly interpreted by recent paleontological findings (Etheridge 1961, Wells and Jorgensen 1964), the desert areas of today, extending from Texas to California, were very different as recently as 10,000 years ago, indicating that sand lizard adaptative radiation must be relatively recent.

Evidence from internal morphology and geographical distribution indicates that earless sand lizards should remain as two closely related groups in the genus *Holbrookia*. Data from comparative skull and throat anatomy, if used alone, indicate a very close relationship between all genera in the sand lizard group, but it is felt that the distinctions, however small, do indicate that *Holbrookia* has evolved from *Callisaurus* stock and has achieved sufficient distinctness to be given generic status. It is, therefore, proposed that sand lizards be classified as they were before *Cophosaurus* was split off by Clarke (1965). This is as follows:

Uma notata Baird
Uma scoparia Cope
Uma exsul Schmidt
Uma paraphygas Williams, Chrapliny, and Smith
Callisaurus draconoides Blainville
Holbrookia texana Troschell
Holbrookia lacerata Cope
Holbrookia maculata Girard
Holbrookia propinqua Baird and Girard

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HYDROLOGICAL FEATURES OF A CALIFORNIA COASTAL FEN

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Abstract.— A unique fen peatland, on the California coast, depends on six streams for its supply of flowing, mineral-rich water. About 25 percent of the water is supplied by surface streams that had average concentrations of Ca^{++} from 0.15 meq/l to 0.32 meq/l and of Mg^{++} from 0.25 meq/l to 0.47 meq/l. During the dry summer period oxygen concentration and pH were lower in the central area than in the fen margins. Water flow near the margins maintains high O_2, pH, and cation content. The fen ranges from 4 m to over 11 m in depth, but the thickest peat layer is made up of very liquid, unconsolidated peat. In one year, an estimated 19.3 metric tons of suspended sediment entered the 38.6 ha fen, which was equivalent to a 42 kg/ha loss from the total watershed.

Inglenook Fen near the coast of Fort Bragg, California, may be the southernmost example of a fen-type peatland on the Pacific coast and is the only recognized example on the California coast (Baker 1972). A fen is a physical land type that has distinctive flora and vegetation. It is often concave in cross section, has strong inflows of mineral-rich waters, has near-neutral pH, contains high amounts of Ca and Mg ions, and is productive (Heinselman 1970). To emphasize the source of minerals and water, this land type is referred to now as a minerotrophic (Heinselman 1970) or rheotrophic (Moore and Bellamy 1973) peatland.

Fens evolve naturally over time to become bogs. Bogs (ombrotrophic peatlands) are characterized as being isolated from mineral-rich water, often convex in cross section, acid in pH, and unproductive (Heinselman 1970). Numerous examples of bogs exist along the Pacific coast of North America (Rigg and Richardson 1938). Several are within a few km of Inglenook Fen in the "pygmy forest" on the upper coastal terraces (Rigg 1933, Jenny et al. 1969).

The peatland type and rate of change from fen to bog is strongly influenced by certain critical or controlling factors. Water sources are the key element in peatland evolution (Heinselman 1970, Moore and Bellamy 1973). Little information is available on the important hydrologic features of Inglenook Fen. Our objectives were to determine the sources and amounts of inflowing water, the nutrient status of the water, and the physical-chemical conditions in the fen.

Study Area

Inglenook Fen was described by Baker (1972), who included a floral list and some chemical conditions. The fen was formed by sand dunes blocking the stream outlet of a small valley on the second coastal terrace. A small 1.11 ha pond (Sandhill Lake) exists at the western edge, and radiating outward, especially to the east, are typical zones of marsh-fen vegetation—floating aquatics, emergents, sedge fen, and woody plants. The fen is 38.6 ha, of which about 4.6 ha are dominated by Cyperaceae fen and *Calamogrostis*-Cyperaceae-*Menyanthes* fen (cf. Baker 1972). The remainder is predominantly woody vegetation (fen carr).

Six streams drain five watersheds (A-E) into the fen (Fig. 1). The watersheds range from forest land (67 percent) and pasture to some residential development in Area C and part of Area D.

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Methods and Materials

Approximately twice a month from November 1972 to November 1973, we measured discharge, water temperature, pH, dissolved oxygen, calcium and magnesium ion content, total suspended sediments, orthophosphate, and nitrate in the fen streams. Silica was measured occasionally. Aerobic limit, peat depth, O_2, pH, and temperature were measured irregularly on the fen.

Flow was measured in two ways. The first involved catching stream flow in a container of predetermined volume. The time required to fill a container was measured with a stopwatch. All streams except A_{no}, A_{so}, and the outlet were measured this way as they emptied from culverts that passed beneath Highway 1 (Fig. 1). Flows of other streams that did not empty from culverts were determined by measuring a section for width, average depth, length, and average velocity. Velocity was determined by timing a float over a measured distance.

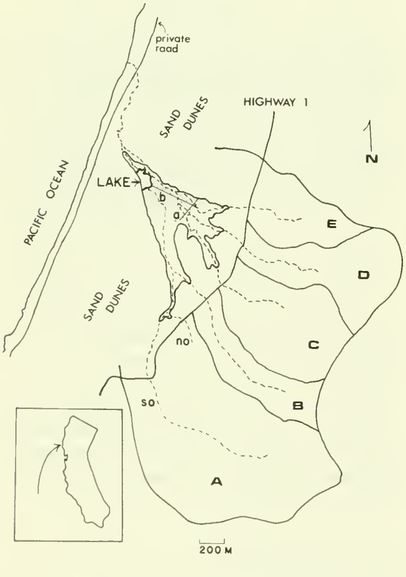

Fig. 1. Map of Inglenook Fen showing inlet streams (dashed lines) and their watersheds (A to E). Lines *a* and *b* are transects for peat depth cores. The dotted area in the central fen region is predominantly sedge vegetation.

Water temperature was determined with a thermistor or mercury thermometer, and oxygen concentration was determined with a YSI Model 51A O_2-temperature meter or by the Winkler method.

Small samples were taken for water pH determinations. Shortly after collection of the sample, pH was measured with a LaMotte colorimetric comparator (wide range pH 3–10, narrow range pH 5–8).

Other water samples were taken for Ca-Mg ions and PO_4-NO_3 analysis. Samples for Ca-Mg analysis were preserved by addition of perchloric acid, filtered qualitatively before analysis, and brought to a concentration of 0.5 meq/l of strontium chloride to reduce interference. Analysis was performed on a Perkin-Elmer Model 303 atomic absorption flame spectrophotometer.

Separate glass bottles were used for PO_4-NO_3 samples; they were stored for one to three weeks in a refrigerator prior to analysis. Determinations were made on a Hach #640 Direct Reading Colorimeter. Orthophosphate was measured by the Hach-Stannaver Method and nitrate (after nitrite adjustment) by the cadmium reduction method.

An additional water sample was vacuum-filtered through a preweighed glass fiber filter (approximately 0.3 μm pore size). The filter was then oven dried and reweighed to determine total suspended sediments.

Silica was measured with a LaMotte colorimetric comparator. The depth to which oxygen was present in the fen (aerobic limit) was determined by measuring the stain that developed on implanted redwood stakes (Erman 1973). The distance from fen surface to where staining begins (absence of oxygen causes stain) is the aerobic limit. To determine peat depth, we made cores along two transects, A and B (Fig. 1), of the fen with a Hiller-type peat borer.

Results and Discussion

Stream Flows

Mean surface flows are given in Table 1. Large seasonal fluctuations occurred in dis-

Table 1. Yearly average (and standard deviations) of environmental conditions of outlet and inlets to Inglenook Fen, Mendocino Co., California.

Environmental Factor			Stream				
	A_{so}	A_{no}	B	C	D	E	Outlet
Discharge (l/sec)	4.93	3.26	14.6	9.17	9.03	4.25	179.8
(S.D.)	(3.97)	(4.93)	(14.1)	(17.7)	(14.8)	(11.5)	(278)
O_2 (mg/l)	10.1	10.0	10.5	10.1	11.3	10.3	7.43
(S.D.)	(1.24)	(2.13)	(0.94)	(1.31)	(1.66)	(1.01)	(1.92)
O_2 saturation (%)	94.4	89.3	101.2	95.1	101.5	95.8	70.5
(S.D.)	(9.47)	(16.8)	(5.56)	(6.3)	(10.7)	(7.64)	(24.4)
Temperature (°C)	12.7	12.0	12.8	12.7	11.3	12.9	13.4
(S.D.)	(3.3)	(3.4)	(3.7)	(4.4)	(4.0)	(4.9)	(5.3)
Median pH	6.5	5.6	6.7	6.8	6.8	6.3	6.6
Ca^{+2} (me/l)	.16	.14	.18	.28	.32	.15	.62
(S.D.)	(.09)	(.08)	(.08)	(.14)	(.15)	(.07)	(.25)
Mg^{+2} (me/l)	.27	.26	.33	.47	.47	.25	.47
(S.D.)	(.06)	(.06)	(.09)	(.14)	(.14)	(.06)	(.10)
Sediments (mg/l)	19.9	11.4	16.0	12.5	16.9	4.24	4.41
(S.D.)	(22.9)	(12.6)	(20.8)	(11.6)	(18.6)	(3.50)	(5.59)
PO_4 -P (mg/l)	.09	.09	.08	.09	.09	.07	.13
(S.D.)	(.08)	(.07)	(.05)	(.08)	(.08)	(.07)	(.08)
NO_3 – N (mg/l)	.60	.23	.28	.13	.28	.06	.12
(S.D.)	(.29)	(.26)	(.07)	(.07)	(.16)	(.03)	(.10)
Conductivity[a] (uMhos @ 25°C)	109	216	154	222	203	92	366

[a] Data from November only.

charge with minimum flows from May to October. Stream B consistently had the highest flow (avg. 14.6 l/sec). The total outflow from May to October (the dry season) averaged 47.6 l/sec (28–68 l/sec) and was more than twice the combined inflow (15.9 l/sec). Mean monthly discharge of the combined inlets and of the outlet are shown in Fig. 2.

One of the most interesting results of this work is the relationship between inlet and outlet flows. R. Jackson (pers. comm.), who surveyed the fen for the Nature Conservancy, surmised that the predominantly sandy soils of the watershed would result in much subsurface flow. For the entire sampling period the measurable surface inflow averaged only 25.2 percent (13.8–66.3 percent) of the measurable surface outflow. With one exception, during a rainstorm on 21 September 1973, measurable inflow never exceeded 50 percent of outflow. Thus subsurface flow appears more important than surface flow in this area. Water, of course, also enters the fen from surrounding sand dunes and direct precipitation on the fen, and it leaves via evaporation and evapotranspiration. These sources were not measured.

By expanding the mean discharge value we estimated the total annual volume of water carried by each stream (Table 2). The estimated yearly inflow of all surface water was 1.43 million m^3, compared to about

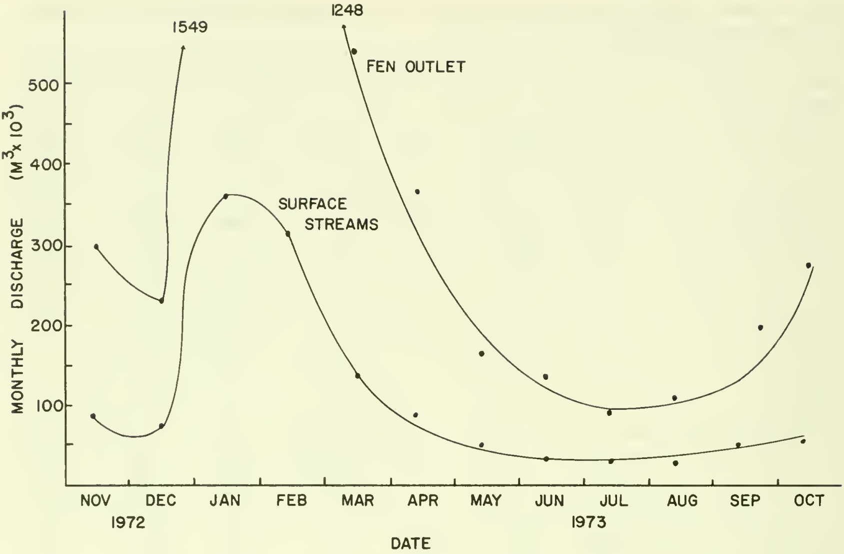

Fig. 2. Estimated total discharge by month of all inlet streams combined and of the outlet.

5.67 million m³ of outflow. In Table 2 the discharge of each inflowing stream is shown as a percentage of the total inflow, and this value is compared with the percentage of the total watershed area for each of the streams. These results indicate differences between size of watershed and amount of surface flow. For example, based on surface flow, Watershed A accounted for 18.1 percent of the water volume while it included 42.7 percent of the total watershed. Watershed B contained 12.4 percent of the area, but accounted for 32.3 percent of the total flow. Differences shown in these figures may be due to differences in vegetative cover, soil type, and slope gradient in the five watersheds. Preliminary soil maps of the fen watershed show streams A to C drain Empire Sandy Loam, while streams D to E drain Hugo Sandy Loam. We have no data on subsurface flow, but it may be that when subsurface flow is added to surface flow, the total contribution of each stream is closer to its percentage of the total watershed.

Mean monthly discharge of the combined inlets and of the outlet are shown in Fig. 2.

TABLE 2. Comparison of surface stream inflow and area of watershed of Inglenook Fen.

Stream	Total Annual Flow ($M^3 \times 10^3$)	% of Total Flow	Area of Watershed (Hectares)	% of Total Watershed Area
A (No + So)	258	18.1	196.3	42.7
B	460	32.3	86.7	12.4
C	289	20.2	33.8	18.3
D	285	20.0	77.7	16.9
E	134	9.4	44.9	1.7
Total	1430		459.4	

Jackson (pers. comm.) has suggested that only Stream E is seasonal. Stream A_{no} was the only intermittent stream during the present study, although Stream E carried less than 0.3 l/sec from June to September.

Temperature and Oxygen

It was impossible to sample the streams at the same time of day on the various dates. Daily fluctuations in temperature are unknown for these streams. As expected, the winter water temperature (5–12 C) was lower than the summer water temperature (15–20 C), although temperatures below 10 C are unusual. High daytime air temperatures are uncommon in summer because of frequent fog along the coast, and thus even small streams are not particularly warm.

In general, oxygen concentration in inlet streams was near air saturation (average 95–101 percent except for A_{no}, which had low O_2 (5.7–7.3 mg/l) at low flows (Table 1). Warmer water temperatures during low flows resulted in lower oxygen concentrations, as shown for Stream B in Fig. 3, than at other times of the year, although oxygen was still near air saturation. For most of the year, the outlet had significantly lower O_2 content than the inlets. The outlet is compared to Stream B in Fig. 3. This result is expected because the fen has a tremendous amount of decaying material that would consume oxygen as water flowed through its length. Much of the inflow water also eventually passes through the small lake near the outlet. Lake O_2 levels were consistently below saturation, especially at lower depths. The outlet stream generally was below 60 percent saturation (less than 7 mg/l) during the wet months; but from June to September, when outflows were less than 50 l/sec, the oxygen levels were at their highest (89–111 percent saturation, 8.4–11.2 mg/l). Higher oxygen content in the outlet during low water periods probably reflects less contact of inflowing water with fen peats. During the winter months water is obviously moving across much of the fen surface. But when inflows diminish to some minimum level (probably at least 50 l/sec combined surface and subsurface), the water tends to move only through the marginal channels ("moats," e.g. Rigg 1940) of the

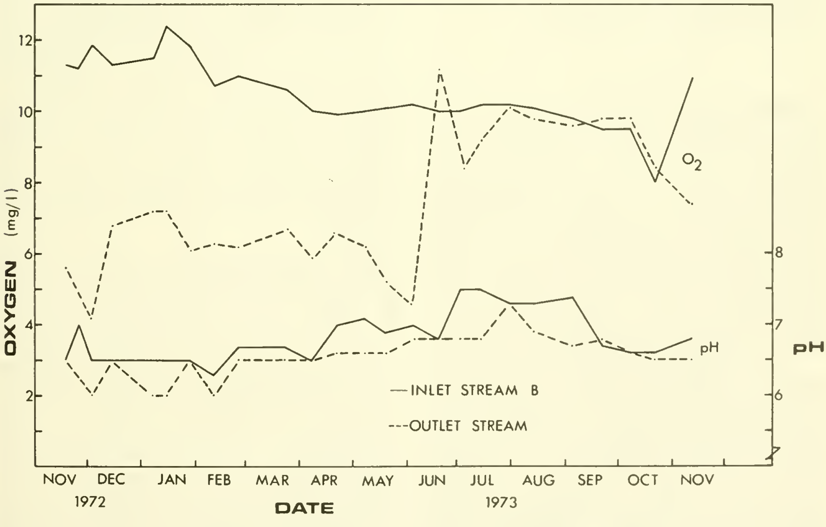

Fig. 3. Seasonal changes in oxygen concentration and pH in the outlet compared to the major inlet stream (B).

fen. We observed that the central sedge area was noticeably drier during the period from June to September, and this observation supports the idea of the sedge area's reduced contact with flowing water and of lower water levels. As long as this oxygen-rich (and relatively mineral-rich) water flows through the central fen, the rate of peat accumulation will be slower than if water flow is confined to the margins. As peat and living plants in the center of a fen become isolated from flowing water, characteristic changes occur (Gorham 1957, Deevey 1958, Heinselman 1970, Moore and Bellamy 1973): the rate of peat accumulation accelerates with a consequent rising of the surface; and the peaty soils become progressively less rich in nutrients, more acid in pH and more bog than fen. Recent work in Manitoba, Canada, showed that about 74 percent of the net primary production of a bog remained after one year, whereas 52 percent remained in a marginal fen (Reader and Stewart 1972). Changes in the biota accompany such changes in physical-chemical conditions. There is, then, a very important influence of the quantity of water and its oxygen and mineral conditions on the rate of succession of Inglenook Fen.

Acidity (pH)

Median pH of the inlet and the outlet streams is given in Table 1. There was a general trend of streams with lower discharge to have lower pH. From May through August, when inflows were derived almost entirely from aquafer rather than run-off, pH was generally above neutral (7.0–7.7) or, in the case of A_{no} and E, was higher than at other periods, although it was less than 7.0. In contrast, streams had lower pH in months when flows were high.

Tests of oxygen, temperature, and pH in the fen were made generally along Transect A. Average values from these collections are given in Table 3. Samples were taken near the fen edge, where moving water occurred all year, as well as toward the center, where water was low in summer and had little flow. These average values showed seasonal changes in oxygen, temperature, and pH that were the opposite of the incoming streams (*see* Stream B in Fig. 3). In winter months high water flushes the entire fen and elevates oxygen and pH (especially in the central region). During drier periods, oxygen and pH decline in the fen except near the marginal channels. Oxygen, pH, and aerobic limit (to be discussed later) are increased relatively close to a region of moving water (Lahde 1969, Heinselman 1970, Erman 1973). Recent studies on a raised bog-system in Germany (Lotschert and Gies 1973, Gies and Lotschert 1973) showed that the marginal fen areas were consistently higher in pH and cation content than the raised, central portion of the peatland.

TABLE 3. Average selected chemical conditions in Inglenook Fen.

Date	Number of Samples	Oxygen (mg/l)	Temp. (°C)	pH
Dec. 2, 1972	7	4.9	9.2	6.0
Jan. 1, 1973	4	5.8	7.1	–
Feb. 10	4	5.8	11.2	6.2
Feb. 24	4	8.7	10.0	6.2
Mar. 24	6	6.2	13.9	6.0
Apr. 7	6	3.5	16.8	6.0
Apr. 21	5	3.5	16.8	5.9
May 10	3	2.6	13.3	6.0
May 19	3	3.0	17.2	5.8
June 19	8	2.5	14.6	5.8
July 2	3	3.3	16.0	5.7
July 14	6	0.7	18.3	5.8
Aug. 1	6	3.0	18.0	5.9
Aug. 13	2	0.6	18.7	5.6
Sept. 4	5	3.0	18.8	5.6
Sept. 21	3	3.4	20.0	6.6
Nov. 3	5	5.0	9.2	5.8

The pH of the outflow stream also indicates isolation of water from the central fen region during dry periods. Instead of pH decreasing—a condition that would occur if the water were in contact with the more acid central area—the pH of the outflow increases (Fig. 3). The studies by Lotschert and Gies (1973) also showed a summer increase in pH and cations in the marginal fen of Schwarze Moor. This change in pH in Inglenook Fen could result from additions of water that drain the alkaline dunes and that are less diluted by stream inflows at this time.

Gorham (1975) suggests a pH of 4.2 as a lower limit of fen conditions, and Lotschert and Gies (1973) give ranges of 4.9 to 6.3 for typical fen conditions. Previous work (Baker 1972) and our present samples from the sedge-fen region indicate pH levels of 5.4 to 6.6, depending on season (more acidic during dry periods).

Calcium-Magnesium ions

Calcium ions averaged 0.15 meq/liter (3 mg/l) at Stream E to 0.32 meq/l (6.4 mg/l) at Stream D (Table 1). These values are lower than observed on one occasion by Baker (1972), who found 0.40 meq/l in Stream E. The outlet was consistently higher in Ca ions (average 0.62 meq/l) than the inlets, and probably reflects the influence of dunes that were found to have higher Ca ion concentration than inflow water (Baker 1972). As a further check on the possibility of the dunes influencing the outlet water, a test for silica was made 7 October 1973. If dune water is important, then silica should be much higher in the outlet than in the inlet streams. The average for the six inlets was 3.5 mg/l, compared to 8.5 mg/l for the outlet. These results further indicate the relative importance of direct drainage from the dunes into the fen margins.

Magnesium ions varied similarly to calcium in all inlet streams (Table 1), and ranged from 0.25 meq/l (E) to 0.47 meq/l (C and D) or 3.5 to 5.7 mg/l. The outlet, however, contained about the same as the inlets (0.47 meq/l), which is in contrast to the situation for calcium as noted previously by Baker (1972).

Sea water spraying directly onto the fen may also contribute to the concentration of various ions in the outflow, as was suggested by Baker (1972).

Heinselman (1970:245) stated that "accumulating evidence indicates that the ionic balance and cation content of peatland waters in relation to water sources and hydrotopography are key factors influencing floristics, vegetation types, and ultimately peatland evolution." He used pH, Ca, and Mg and specific conductivity of peatland waters to relate peatland types and vegetation. We used overall averages of the six inlet streams for these factors and obtained these figures: pH = 6.5, Ca = .205 meq/l (4.1 mg/l), Mg = .342 meq/l (4.16 mg/l), and specific conductivity (measured in November only) = 166. These values indicate minerotrophic to weakly minerotrophic waters in Heinselman's classification (1970), and they are typical also for European fen conditions (Lotschert and Gies 1973).

Sediments

Mean sediment concentrations in the six inlet streams and the outlet are given in Table 1. Stream A_{so} had the greatest average sediment load (19.9 mg/liter), and Stream E had the lowest (42. mg/liter). The average from all inlets was considerably higher than the outlet (13.5 mg/l inlets, 4.4 mg/l outlet). On an annual basis this sediment influx is approximately 19.3 metric tons entering the fen and 25 metric tons leaving. The greater amount of sediments leaving than entering results partly from the influx of dune material near the outlet, where dunes encroach directly on the stream. Natural dune shifting, in addition to disturbance from off-road vehicles on the dunes, causes sands to be mobile in the vicinity of the fen. The small existing housing development consisting of 13 houses in Watershed C and part of Watershed D and occasional plowing of some pastures as yet show little impact on stream-suspended sediments.

One of the major factors that influences the rate of fen-bog succession is the rate of basin filling. This filling occurs from peat accumulation, dune shifting, and sedimentation from the watershed. Soil disturbance in the watershed can rapidly increase the amount of sediments reaching the inlet streams and, subsequently, the fen.

Most of the incoming sediments no doubt accumulate in the fen, but our methods cannot distinguish the net change. The rate of sediment loss from the entire watershed (459.4 ha) amounts to 42 kg/ha per year. In a study of the Hubbard Brook Watershed in New Hampshire, Bormann et al. (1969) found that particulate losses from a forested watershed were 25 kg/ha per year, and a summary of studies on small, undisturbed forested watersheds gave a range from 25 to 53 kg/ha (Likens and Bormann 1974).

Phosphate and Nitrate

Soluble phosphate-phosphorus (Table 1) was very similar in most of the inlet streams (.07–.09 mg/l) and was slightly higher in the outlet streams (.13 mg/l). This result suggests that PO_4-P is being released by decomposition in the fen. Occasionally, every stream contained three to five times the average PO_4-P found in other streams, but these higher levels occurred in no consistent pattern. They may have resulted from agricultural activities, since pastureland is occasionally fertilized, but the intermittent nature of the higher readings does not suggest sewage contamination.

Nitrates seem to be retained in the fen (Table 1). The average amount of NO_3-N in the outlet (0.12 mg/l) was considerably lower than in most of the inlets. Nitrates were also occasionally high in each stream, although A_{so} was consistently higher in NO_3, and this result suggests some basic difference in the immediate vicinity of A_{so} because A_{no} did not appear similarly influenced. A yellow color in A_{so} water may have interfered with colorometric determinations.

The few homes on Watershed C and Watershed D apparently had no major effect on PO_4 or NO_3 in those streams. The levels of these nutrients in the six streams may serve as a baseline in case of later development.

Peat Depth and Aerobic Limit of the Fen

Two series of cores to determine peat depth were taken along the transects shown in Fig. 1. Transect A was taken across the fen at 30 m intervals (Fig. 4). Maximum peat depth was 8.2 m along this transect. The peat was composed of three distinct layers: a narrow surface layer of dense living plant roots and organic matter; a layer

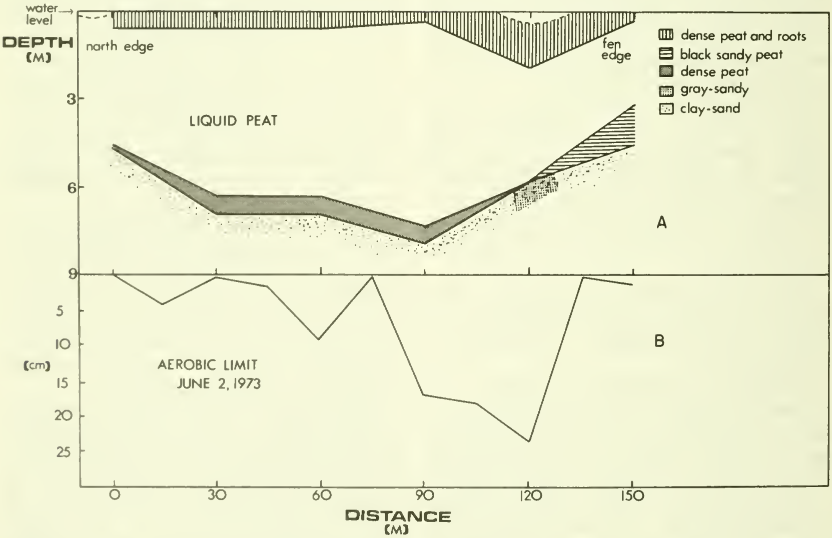

Fig. 4. Peat depth profile (A) along transect *a* at 30 m intervals and aerobic limits (B) along the same transect at 15 m intervals. Dotted lines near surface of A indicate approximate location of stream channels.

underlying the surface made up of loose, soft brown peat that was very liquid; and a basal layer of dense peat in the central fen region. When the peat borer cut through the surface layer of dense fibrous peat, water squirted up through the hole, especially on the southern edge. The corer then passed freely through the next layer without effort until the bottom peat layer was reached. It appeared that the entire surface was floating over the liquid middle layer, and exerted a pressure on the watery fluid below.

Beneath the peat was a dark clay layer, except on the southeastern edge (0–30 m), where black organic ooze overlaid the dark clay layer directly below the surface channel.

Along this same transect, a series of measures of aerobic limit were taken (2 June 1973) every 15 m. The influence of moving water is apparent in the aerobic limit measures; the limits tend to be deeper where moving water maintains higher O_2 levels, and hence maintains deep O_2 penetration (Fig. 4). Mean aerobic limit for the 11 samples was 7.1 cm.

A second transect to determine peat depth was taken along the east-west axis of the fen (Fig. 5) and ended at Sandhill Lake. The layers of peat are similar to those in Fig. 4. Fen depth increased toward the lake, where depths exceeded 11 m, the limit of our coring device. This transect halfway along its length also revealed a ridge covered with dark sand on the bottom. The higher sand-topped ridge may be the remnant of a former dune now submerged by the fen.

Depth measures of Sandhill Lake showed that it had vertical sides that drop off rapidly to about 6 m. The peat beneath the lake was of the same loose, watery texture as the similar layer in the fen and extended beyond the 11 m limit of our device. Peat profiles of bogs along the Pacific coast made by Rigg and Richardson (1938) showed some bogs with lakes that had similar steep sides and were relatively deep in comparison to the total bog depth. Heinselman (1970) showed that even small lakes surrounded by peat may persist for long periods. Early workers on bog lakes believed that the lakes were in terminal stages of succession and would soon fill. While this conclusion may still be valid over a very long time period, Heinselman (1970) showed that Myrtle Lake in Minnesota had maintained its size and depth and had even risen, rather than filled, with the height increase of the surrounding peat.

Under existing conditions Inglenook Fen

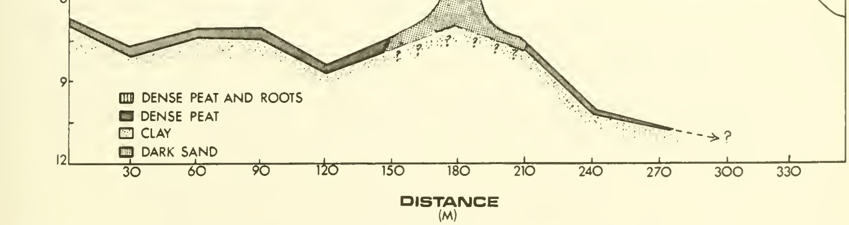

Fig. 5. Peat depth profile along transect *b*. Note sandy ridge at 180 m that may be a remnant sand dune. Coring device could not extend beyond 11 m near the lake.

is slowly filling, and during low flows it shows signs of succession toward bog (ombrotrophic peatland). The process of change from minerotrophic to ombrotrophic would still require a very long time. But as recent studies of lake eutrophication have shown, a natural successional change in productive status can be tremendously increased by man's activities. The data in this report provide baseline information on some of the key elements essential to maintenance of a minerotrophic peatland.

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INTRODUCED AND EXPORTED AMERICAN SCOLYTIDAE (COLEOPTERA)[1]

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Abstract.—Fourteen North, Central, and South American Scolytidae have reached areas outside of America, namely Hawaii (5), Australia (3), Southeast Asia (2), Africa (7), Europe (1), and worldwide (1). The 44 species introduced into North and Central America have originated in South America (10), Southeast Asia (15), Africa (14), or Europe (7). Four North and Central American species have extended their ranges into new territory within this region. Most of the species that breed in the bole or roots of their host were imported more than a half century ago; those imported since 1950 breed mostly in seeds, pods, dry fruits, or small branches. Forty-five of the 62 species apparently can reproduce by means of facultative arrhenotokic parthenogenesis.

A brief report on the extraterritorial distribution of American Scolytidae to the Fourteenth International Congress of Entomology (Wood 1972) aroused interest sufficient to prompt a more comprehensive review. This report omits those species that have moved into or out of North and Central America through natural migration. Those species intercepted in routine border inspection and not actually established in an extraterritorial locality are also omitted. This report includes only those species for which I have examined specimens taken from a breeding population in an extraterritorial locality. In most instances the introductions to new areas have occurred within the past century, and the spread of each species is part of the historical record. In other cases the entry and spread was not recorded, and the importation is based on undocumented circumstantial evidence. An account of the nomenclature, distribution, hosts, classification, etc., will be published in my monograph of North and Central American Scolytidae (currently in preparation). The documentation for the many items cited below will appear in the monograph.

Of the 62 species listed here (Table 1), six are native North or Central American species that were introduced to another extraterritorial part of North or Central America. The 14 species exported from North, Central, and South America have reached the following areas (some have reached more than one area):

Hawaii 5	Africa 7
Australia 3	Europe 1
S.E. Asia 2	Worldwide 1

Of the 44 species imported into North and Central America, probable areas of origin are (three Asian species also occur in Africa):

South America 10	Africa 14
S.E. Asia 15	Europe 7

The 62 species treated here are sorted on the basis of the host material usually selected for the excavation of breeding tunnels as follows:

Roots	2
Bole or logs	11
Twigs and branches	28
Both seeds and branches	7
Seeds, pods, dry fruits	10
Misc. branches, weeds, herbs, etc.	2
Fruiting stalks of grass	1
Unknown	1

Almost all of the imported species that breed in roots, logs, or boles were established in North and Central America a half century or more ago. Those species imported since about 1940 breed almost exclusively in seeds, pods, or other dry fruit-

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TABLE 1. North and Central American Scolytidae that have been introduced from or exported to foreign lands.

Species	Probable origin	Introduced to	Host material
Araptus politus	Mexico, C. America	Florida, Antilles	Seeds
Coccotrypes aciculatus	New Guinea?	Panama and Brazil	
" *advena*	S.E. Asia, Indonesia	Cuba to S. America	Seeds or branches
" *carpophagus*	Africa?	Florida to S. America	Seeds
" *dactyliperda*	Africa?	USA to S. America	Seeds
" *distinctus*	Ceylon?	Florida to S. America	Palm fruits
" *indicus*	S.E. Asia	Florida to S. America	Seeds
" *rhizophorae*	Indonesia	Florida, Galapagos Islands	Mangrove "seeds"
Corthylus spinifer	C. and S. America	Florida	Branches or seedlings
Cryphalomorphus jalapae	Mexico	Worldwide interceptions	Jalapa root
Cryptocarenus heveae	C. and S. America	Africa, Florida	Branches, etc.
" *seriatus*	S. America	Florida, Antilles	Branches, etc.
Crypturgus pusillus	Europe, Asia	E. North America	*Picea* boles
Dendroctonus frontalis	USA	Honduras	*Pinus* boles
Gnathotrichus materiarius	E. North America	France	*Pinus* boles
Hylastinus obscurus	Europe	N. America	Clover roots
Hypocryphalus mangiferae	India	Florida to S. America, etc.	*Mangifera indica*
Hypothenemus aequaliclavatus	Indonesia	Honduras, Jamaica	Unknown
" *africanus*	S. Africa	USA to S. America	Fruits, branches
" *areccae*	S.E. Asia	Florida to S. America, etc.	Seeds, branches, etc.
" *birmanus*	S.E. Asia	Florida, C. America, etc.	Branches
" *brunneus*	Africa?	USA to Trinidad	Branches
" *californicus*	Africa?	USA to Mexico	Twigs, etc.
" *columbi*	Africa?	USA to S. America	Twigs, weeds, etc.
" *crudiae*	S.E. Asia?	USA to S. America	Twigs, weeds, etc.
" *cylindricus*	Africa?	Mexico to S. America	Branches
" *erectus*	Africa?	USA to S. America	Branches
" *eruditus*	Tropical America?	Almost cosmopolitan	Twigs, seeds, etc.
" *hampei*	Africa	C. and S. America, etc.	Coffee berries
" *javanus*	Africa?	Florida to S. America, etc.	Branches, pods
" *obscurus*	Tropical America	Intercepted worldwide	Brazil nuts, etc.
" *parallelus*	Mexico	Hawaii	Twigs?
" *pubescens*	Tropical America?	Florida, Hawaii, etc.	Grass
" *seriatus*	Tropical America?	USA, Africa, etc.	Twigs, seeds, etc.
" *setosus*	Africa?	Antilles to S. America	Fruits, pods, etc.
Ips grandicollis	N. America	Australia	*Pinus* limbs, etc.
Microborus boops	C. America	Africa, Jamaica	Branches, etc.
Pagiocerus frontalis	S. America	USA, etc.	Seeds
Phloeosinus cupressi	N. America	Panama, Australia, etc.	*Cupressus* branches
Pityophthorus confusus	USA	Honduras	*Pinus* bole
" *juglandis*	Arizona	California	*Juglans* branches
Premnobius cavipennis	Africa	Florida to S. America	Limbs, etc.
" *ambitiosus*	Africa	S. America	Limbs, etc.
Scolytus mali	Europe	N. America	Fruit trees
" *multistriatus*	Europe	N. America, etc.	*Ulmus* limbs, etc.
" *rugulosus*	Europe	N. America, etc.	Fruit trees
Xyleborinus aspericauda	C. and S. America	Florida	Limbs, logs
" *saxeseni*	Europe	N. America, etc.	Limbs, logs, etc.
Xyleborus affinis	Tropical America	Hawaii to Malaya, Africa	Logs, etc.
" *dispar*	Europe	N. America	Limbs, etc.
" *ferrugineus*	Tropical America	Hawaii to Australia, Africa	Logs
" *obliquus*	S. America?	N. America, Africa	Branches
" *rubricollis*	S.E. Asia	N. America	Branches, boles, etc.
" *spinulosus*	Tropical America	Hawaii	Limbs
" *validus*	S.E. Asia	New York	Limbs, etc.
" *volvulus*	Tropical America	Hawaii to Malaya, Africa	Logs
" *xylographus*	E. North America	California	*Quercus* logs
Xylosandrus compactus	S.E. Asia?	Florida, Cuba, Africa, etc.	Twigs
" *crassiusculus*	S.E. Asia	South Carolina, Hawaii	Branches
" *germanus*	Japan	USA	Limbs, etc.
" *morigerus*	S.E. Asia	C. and S. America	Branches, etc.
" *zimmermanni*	Tropical America	Florida	Branches

ing structures or in small branches. It is of interest that 45 of the 62 species can reproduce by means of facultative arrhenotokic parthenogenesis, by which means one female can establish an entire breeding population.

Araptus politus Blandford, 1904, is native to southern Mexico and Central America, where it breeds in *Mucuna* seeds. It has been taken in Haiti (Cola nuts), Jamaica and Cuba (host not recorded), and Miami, Florida (intercepted in "bird seed"; breeding in "seeds") since 1960.

Coccotrypes aciculatus Schedl, 1952, was named from New Guinea. It has been taken in Brazil (Cuma nuts), Costa Rica, and Panama (at light) since 1938. Its hosts and habits are unknown.

Coccotrypes advena Blandford, 1894, is apparently a native of Indonesia. It has been taken in India, Java, Japan, Micronesia, Samoa, Hawaii, Surinam, and Cuba since 1915. It breeds in either bark or large seeds of a variety of tropical hosts.

Coccotrypes carpophagus (Hornung, 1842) was named from betel nuts from India, although it probably originated in Africa. It has spread to virtually all tropical and subtropical areas of the world, where it breeds in a wide variety of nuts and other large seeds. It is commonly intercepted throughout the world, but in North America it breeds permanently only in southern Florida and Mexico.

Coccotrypes dactyliperda (Fabricius, 1801) is probably of African origin. It breeds in virtually all tropical and subtropical areas of the world. It is most common in date pits, but may breed in a wide variety of nuts, seeds, and buttons or other objects made from vegetable ivory. It breeds in Florida and Arizona and probably in other southern states.

Coccotrypes distinctus (Motschulsky, 1866) was named from Ceylon, where it probably originated. It has also been reported from Micronesia, Hawaii, Honduras, Puerto Rico, British Guiana, and southern Florida, where it breeds in a wide variety of palm seeds.

Coccotrypes indicus (Eggers, 1936) was named from India. It is widely distributed in southeastern Asia and Indonesia, and has been reported from the Fiji Islands, Tahiti, Hawaii, Brazil, Surinam, Trinidad, Puerto Rico, Martinique, Guadeloupe, Costa Rica, Panama, and Coral Gables, Florida. It has been intercepted in various seeds at several American ports. It probably is capable of breeding in large seeds in most southern states of the U.S.A.

Coccotrypes rhizophorae (Hopkins, 1915) is apparently from Indonesia. It also breeds in the Galapagos Islands and southern Florida. It infests the viviparous seeds of mangrove (*Rhizophora mangle*).

Corthylus spinifer Schwarz, 1891, was named from Florida, but it is very doubtful that it is a native species. In addition to Florida, its present distribution extends from Brazil to Veracruz, Mexico. Several related species occur in Central America and northern South America. In all probability, it has spread through commerce to Brazil and Florida in the past century.

Cryphalomorphus jalapae (Letzner, 1848) is native to Mexico, where it breeds in jalapa root (presumably *Exogonium jalapa*). It is not known to be permanently established in any invaded territory.

Cryptocarenus heveae (Hagedorn, 1912) was named from Africa (Congo), where it damaged rubber trees. It is now known to be native to Mexico, Central America, and northern South America. It also breeds in Ghana, Congo, Brazil, Jamaica, Cuba, and southern Florida. It infests the pith of small, broken, or unthrifty stems of a wide variety of trees, shrubs, and woody vines.

Cryptocarenus seriatus Eggers, 1933, is probably native to Bolivia and Peru, but now occurs throughout South America, Central America, Mexico, Jamaica, Haiti, the Virgin Islands, Cuba, Florida, and southern Texas. It appears to have entered the United States since 1930 and to have reached Central America and Mexico after 1915 but prior to 1953. It breeds in the small branches of a wide variety of trees, shrubs, and woody vines.

Crypturgus pusillus (Gyllenhal, 1813) is native to Europe, north Africa, and northern Asia. It was apparently introduced to eastern Canada and/or the northeastern United States in the colonial period. It is a secondary enemy of spruce (*Picea*), and breeds from Ontario and Newfoundland to New Jersey in the bark of the bole and larger branches of the host.

Dendroctonus frontalis Zimmermann, 1868, is native to the southern United States, where it is a primary enemy of pine (*Pinus*). It was evidently introduced into Honduras between 1910 and 1964. It occurs in the same trees with *D. mexicanus*, with which it is easily confused. A simultaneous introduction of *Pityophthorus confusus* Blandford apparently occurred. Recent collections (not seen) report this species from southeastern Mexico. If correct, these records indicate that this species reached Honduras by natural migration and not through commerce.

Gnathotrichus materiarius (Fitch, 1858) is native to eastern North America, where it is a secondary enemy of pine (*Pinus*). Shortly before 1936 it was introduced into France. Since then it has spread into neighboring areas, and may eventually occupy the entire pine belt of Europe and Asia. It is a wood-boring ambrosia beetle.

Hylastinus obscurus (Marsham, 1802) was introduced to North America (New York) from Europe sometime prior to 1878. By 1929 it had reached British Columbia and Oregon. It now occurs in all provinces and states where alfalfa or other forage clovers are grown.

Hypocryphalus mangiferae (Stebbing, 1914) is apparently native to India, but it has spread throughout the tropical regions of the world wherever its host, *Mangifera indica*, is cultivated. It was recorded from Guadeloupe Island in 1872 and was taken in Florida in about 1949. It is common throughout southern Mexico and Central America.

Hypothenemus aequaliclavatus Schedl, 1939, was named from Indonesia. A specimen was taken in Honduras in 1906 and another in Jamaica in 1967. Nothing more is known of this species.

Hypothenemus africanus (Hopkins, 1915) was named from South Africa, where it probably originated. Since 1933 it has been reported from Indonesia, Malaysia, Brazil, Venezuela, Jamaica, Bahama Islands, Dominican Republic, Puerto Rico, Honduras, Alabama, and Louisiana. It breeds in the twigs and fruiting pods of various trees, shrubs, and vines.

Hypothenemus areccae (Hornung, 1842) is apparently native to southeastern Asia. It now occurs in virtually all tropical and subtropical countries in the world. The first record of its occurrence in America was in Brazil in 1928. It now occurs throughout South America, Hawaii, Martinique, the Virgin Islands, Puerto Rico, the Bahama Islands, and southern Florida. It breeds in seeds, dry fruits, twigs, and in a wide variety of other materials. At times it becomes a serious pest of mature seeds and nuts and stored products.

Hypothenemus birmanus (Eichhoff, 1878) was named from Burma, where it probably is native. It has been reported from southeast Asia, Indonesia, the Philippine Islands, Australia, Micronesia, Hawaii, Jamaica, Central America, Mexico, and Florida. It breeds in the twigs and small branches of a wide variety of trees, shrubs, and woody vines. It was first taken in Jamaica in 1937 and in Florida in 1951.

Hypothenemus brunneus (Hopkins, 1915) occurs from Alabama, Florida, and Texas to Panama, including the Bahama Islands, Cuba, Puerto Rico, the Virgin Islands, and Trinidad. It has no native American relatives, but several similar species are native to Africa. For this reason it is presumed to be of African origin. It was first reported from Texas in 1915.

Hypothenemus californicus Hopkins, 1915, was regarded as a native North American species until specimens were taken recently in Liberia and Israel. Since it is not allied to any American species, but has several near relatives in Africa, it is presumed to be of African origin. It occurs from southern California to New Jersey and southward to southern Mexico.

Hypothenemus columbi Hopkins, 1915, was named from the southern United States and has since been reported from Mexico, Costa Rica, Colombia, Venezuela, Cuba, and the Bahama Islands. All representatives of this species group are of Old World origin. It is presumed that this species also will eventually be found in Africa. It breeds in a wide variety of materials, including twigs, weeds, straw, seeds (rare), etc. It is of some economic importance.

Hypothenemus crudiae (Panzer, 1791) was named from India, but it has spread through commerce to virtually all tropical and subtropical areas of the world for so long that its true origin is unknown. It is common from the eastern United States to Argentina. Circumstantial evidence suggests a southern Asian origin. Although it breeds in small branches of trees, shrubs, vines, weeds, or other plants, its greatest populations occur in seeds, pods, or other fruiting bodies, where it has caused much economic damage in mature seeds both in the field and in storage. Its importance in agriculture or forestry is limited to its effect on seed production.

Hypothenemus cylindricus (Hopkins, 1915) was named from Guatemala, but is now known from Mexico to Panama, Colombia, Venezuela, Guadeloupe, and Africa (Liberia). Since this species has no close relatives native to America, it is presumed that it is of African origin where several near relatives occur. It breeds in small branches of trees, shrubs, and vines.

Hypothenemus erectus LeConte, 1876, was named from Texas, but it is now known from Texas to Honduras, Venezuela, Cuba, the Virgin Islands, and Africa. Several very closely related forms occur in Africa, but there are no known native American species that are closely related For this reason it is presumed to be of African origin. It breeds in small branches of a wide variety of trees and shrubs.

Hypothenemus eruditus Westwood, 1836, is probably the most widely distributed and most frequently encountered scolytid species in the world. It is known from virtually all tropical and subtropical areas of the world and in temperate regions where sufficient moisture and vegetation are present. It breeds in the bark of the trunk or branches of numerous plants, in flowers, weeds, grass, fruiting bodies of fungi, and seeds; the original series was breeding in the cover of an old book. In America it is known from Michigan to Argentina as a common species. It probably originated in the American tropics. It is frequently of economic importance in mature seeds or pods both in the field and in storage.

Hypothenemus hampei (Ferrari, 1867) is the notorious coffee berry borer. It is apparently native to Africa, but it occurs throughout the coffee-growing regions of the Old World and in Brazil. More recently it has reached Colombia and Guatemala. It breeds only in coffee beans. Infested beans have been intercepted in most countries of the world. It is of great economic importance.

Hypothenemus javanus (Eggers, 1908) was named from Indonesia, although it may have originated in Africa. It is now known from Africa (Camerouns, Congo, Ghana, and Liberia), Indonesia, the Philippines, Mexico to Panama, Colombia, Venezuela, Guadeloupe, Puerto Rico, Cuba, and Florida. It breeds in small branches and seed pods of a wide variety of plants. It has been of economic concern in some situations.

Hypothenemus obscurus (Fabricius, 1801) originated in the American tropics. It breeds from Costa Rica and Puerto Rico to Brazil, but has been intercepted in seeds and nuts in most countries of the world. It is best known as a borer in Brazil nuts, although it breeds in a wide variety of seeds and dry fruits and, apparently, can reproduce in bark (uncommon). It is an important pest of many tropical nuts and fruits. Breeding populations in Florida apparently hybridize with the native *H. seriatus* (Eichhoff) and are absorbed by that species.

Hypothenemus parallelus (Hopkins, 1915) was named from Mexico, where it may have originated. It is also known to occur in Hawaii. It is very similar to *H. eruditus* Westwood, and may be no more than a morphological variation of that species.

Hypothenemus pubescens Hopkins, 1915, was named from Florida, but it is now known to occur in Texas, Puerto Rico, Mexico, and Hawaii. Because of its very small size and its unusual habit of breeding in the fruiting stalks of grass (*Andropogon*, *Cynodon*, and *Paspalum*) it probably has been overlooked. An American origin is suspected.

Hypothenemus seriatus (Eichhoff, 1871) was named from Louisiana. It occurs from West Virginia to Brazil, Hawaii to Australia, Indonesia, Madagascar, and Africa (the Ivory Coast). It is probably of American origin. It breeds most commonly in twigs and small branches, but may also occur in seeds, pods, weeds, or other plant material. It is of economic concern.

Hypothenemus setosus (Eichhoff, 1867) was named from Guadeloupe, although it is probably native to Africa. It occurs from Mexico to Brazil, Guadeloupe, Puerto Rico, and Africa (Camerouns, Congo). It breeds in small branches and fruiting bodies of a wide variety of hosts.

Ips grandicollis (Eichhoff, 1868) occurs from southern Manitoba and Quebec to Florida and Honduras. It was introduced into pine plantations in Australia. It is of economic concern.

Microborus boops Blandford, 1897, is a rare species that is known from Guatemala to Panama. Its occurrence in Jamaica probably represents an introduction. It was also introduced into Africa (Camerouns, Gold Coast, Uganda) prior to 1919.

Pagiocerus frontalis (Fabricius, 1801) probably originated in southern South America, where similar species occur. It has spread northward in America to North Carolina and Texas, and it is occasionally intercepted in corn (maize) in Europe and elsewhere. In the Andean region of South America it is a significant pest of dry mature corn in the field and in storage.

Phloeosinus cupressi Hopkins, 1903, is native to the coastal region from Alaska to California, where it breeds in *Cupressus* and a few related tree genera. It has been introduced into Panama, Australia, and New Zealand.

Pityophthorus confusus Blandford, 1904, is apparently native to the southeastern United States, where it occurs in *Pinus* boles with *Dendroctonus frontalis* Zimmermann. It appears to have reached Honduras with *D. frontalis* either by natural migration or through commerce (see *D. frontalis* above).

Pityophthorus juglandis Blackman, 1928, infests native black walnut (*Juglans*) in southern Arizona and New Mexico. It was reported as new to California by Bright and Stark (1973). Since native potential hosts occur in the area, there is a question as to whether an oversight in collecting prior to 1959 occurred or an introduction actually did occur.

Premnobius cavipennis Eichhoff, 1878, is native to Africa, where it is a common, widely distributed species. Prior to 1931 it was introduced into South America and has now spread northward to southern Mexico (1951) and Florida (1939). It is an ambrosia beetle that breeds in a wide variety of hosts in material about two to eight inches in diameter. It may be of some economic concern.

Premnobius ambitiosus (Schaufuss, 1897) has not yet been reported from North or Central America, although it probably occurs there. It is native to Africa, but was introduced into Brazil and Colombia prior to 1958. It is now known from Bolivia and has probably reached most other South and Central American countries. Its habits and importance apparently are similar to those of *P. cavipennis*.

Scolytus mali (Bechstein, 1805) is native to Europe, where it is a pest of apples, pears, prunes, and other cultivated fruit trees. It was introduced into New York prior to 1868 but was virtually unknown here until about 1950. Since then it has spread into southern Ontario, Michigan, Ohio, and Maryland and should spread into most of the states in the U.S.A. within a few years. It is larger than *S. rugulosus*, but apparently has similar habits.

Scolytus multistriatus (Marsham, 1802) is native to temperate Europe and Asia. It was introduced into North America and now occurs in all of the 48 contiguous states of the U.S.A. and is apparently in all of the southern provinces of Canada. It is the well-known European elm bark beetle, the principal vector of Dutch Elm Disease. It has also been introduced into several other areas of the world where elms grow.

Scolytus rugulosus (Müller, 1818) is the shot-hole borer of cultivated fruit trees. It is native to Europe and Asia, but it was introduced into North America very early in the settlement of this continent and now occurs in all states and provinces where apples are grown.

Xyleborinus aspericauda (Eggers, 1941) is native to Central and South America. One specimen was taken in the field in southern Florida (Biscayne Bay). Whether or not it is established in Florida is not known. It is an ambrosia beetle that breeds in the limbs and logs of a wide variety of host plants.

Xyleborinus saxeseni (Ratzeburg, 1837) is native to Europe, but has been transported to most temperate areas of the world. In North America it has been reported from 33 states of the U.S.A., from British Columbia, and from Baja California. It is probably more widely distributed, but has been overlooked due to the lack of collecting. It was also intercepted in Australia in logs from Brazil and it has been in Hawaii for many years. In desert areas it is of little or no economic concern, but may be a significant pest elsewhere.

Xyleborus affinis Eichhoff, 1868, is probably native to tropical America, but now occurs from Massachusetts to Argentina, from Hawaii to Malaya, and in Africa. It breeds in injured, dying, and cut trees and is a significant pest of logs. It does not normally breed in sawed lumber.

Xyleborus dispar (Fabricius, 1792) is native to Europe, but was introduced into North America prior to 1817. It is now widely distributed in southern Canada (Nova Scotia to British Columbia) and in the northern United States (south to Virginia and Utah). It is an ambrosia beetle that breeds in a wide variety of hosts in material two to ten inches in diameter. It is of economic concern in some areas.

Xyleborus ferrugineus (Fabricius, 1801) probably originated in tropical America, but it has now spread to Arizona, Michigan, and Massachusetts in the continental United States, as well as Hawaii, Micronesia, Australia, and Africa, and may have reached other tropical areas where it has not yet been detected. Its habits are similar to those of *X. affinis* except that it is more aggressive and more abundant and, consequently, is of greater economic concern.

Xyleborus obliquus (LeConte, 1878) was named from Florida, but it is probably of South American origin where it and similar species occur. It now occurs from Virginia to Brazil and in Africa (Congo and Zambia). It apparently breeds in unthrifty or cut branches of a wide variety of hosts. In the United States it has been reported from the District of Columbia, Florida, Georgia, Mississippi, and Virginia; in Mexico from Michoacan; in Central America from Guatemala; and in South America from Colombia and Brazil.

Xyleborus rubricollis Eichhoff, 1875, is native to southeastern Asia from Malaya to Japan. It was introduced into the United States prior to 1942, where it has been reported from Connecticut, Maryland, and Virginia. It is an ambrosia beetle that breeds in a wide variety of hosts. It may be of local economic concern in some areas.

Xyleborus spinulosus Blandford, 1898, is native to tropical America from central Mexico to Brazil. It was introduced into Hawaii prior to 1934. It breeds in the branches of a wide variety of host trees, shrubs, and woody vines.

Xyleborus validus Eichhoff, 1875, was named from Japan; it has also been reported from Taiwan and China. About 1975 it became established in New York. In recent years it has been intercepted from wooden packing crates of Japanese origin at numerous ports worldwide. It is anticipated that it will become established in additional areas in the near future.

Xyleborus volvulus (Fabricius, 1775) occurs in two geographical races that probably ranged from the coastal southeastern United States to Argentina. One or both races, including hybrids between the two, have spread to Hawaii, Micronesia, Australia to Malaya, Africa, and Madagascar. Its habits are similar to *X. affinis* and *X. ferrugineus* except that it is usually less abundant. It is of some conomic concern.

Xyleborus xylographus (Say, 1926) is native to eastern North America from Ontario and Quebec to the Gulf Coast and Cuba. A few very old specimens labeled "Brazil" and "Chile" have been examined, but they are assumed to be mislabeled. One specimen from China Flat, Eldorado County, California (1948), apparently represents a new introduction. It breeds in *Quercus*, rarely in other trees.

Xylosandrus compactus (Eichhoff, 1874) occurs from Hawaii to Sri Lanka (Ceylon) and Japan, Africa, Cuba (1958), Mississippi (1968), Georgia (1975?), and Florida (1941). It is probably of Asian origin. It is an aggressive primary borer in new, vigorous twig terminals in a wide variety of hosts. It has significant economic importance. When I reported the identity of this species personally in 1952 to United States Department of Agriculture officials, I was told: "Suppress the information. We already have too many problems to worry about." At the time, its distribution was very local in Florida and eradication would have been comparatively simple. It is widely known as the black shot-hole borer. It may be of extreme economic importance in some areas.

Xylosandrus crassiusculus (Motschulsky, 1866) is native to the Indo-Malayan region. It now occurs in Africa, Hawaii, Australia, and South Carolina (1974). It is an ambrosia beetle that breeds in branches and limbs of a wide variety of hosts. It has some economic importance.

Xylosandrus germanus (Blandford, 1894) was named from Japan. It was introduced into the United States prior to 1931 and it now occurs from Illinois and Connecticut to West Virginia. It breeds in a wide variety of hosts from the branches to the stump. It may be of local economic concern.

Xylosandrus morigerus (Blandford, 1894) is native to southeastern Asia and Indonesia. It was introduced into America prior to 1959 and now breeds from Mexico (Veracruz) to Colombia and Venezuela. It has been intercepted in ports of entry in Arizona, California, and New Jersey, but breeding populations are not yet known from the United States. It is an ambrosia beetle that breeds in small stems of a wide variety of trees, shrubs, vines, and herbaceous plants. It has some economic importance. It is widely known as the red shot-hole borer.

Xylosandrus zimmermanni (Hopkins, 1915) is probably native to northern South America and Central America. It apparently was introduced into southern Florida prior to 1915. It is rather uncommon in small branches of trees, shrubs, and vines of a wide variety of plants. It is of minor economic concern.

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THE SAGEBRUSH VOLE FLEA, *MEGABOTHRIS CLANTONI PRINCEI*, IN WESTERN UTAH, WITH COMMENTS ON THE DISTRIBUTION OF *MEGABOTHRIS* IN THE BONNEVILLE BASIN

Harold J. Egoscue[1]

Abstract.— The sagebrush vole flea (*Megabothris clantoni princei* Hubbard) is reported from Utah for the first time, based on collections made in Tooele County. Distribution of the flea *Megabothris abantis* in the Bonneville Basin is limited to the Oquirrh Mountains, where its presence appears to be determined by the occurrence of the western jumping mouse.

Fleas previously recorded from the sagebrush vole, *Lagurus curtatus intermedius* (Taylor), in western Utah included *Amphipsylla sibirica* ssp. "near" *washingtona* (Egoscue 1966), a primary sagebrush vole flea described from eastern Washington (Hubbard 1954). This note reports the occurrence of a second sagebrush vole flea in Utah, *Megabothris clantoni princei* Hubbard, with a range extension of about 604 km east-southeast from the type locality, 6.4 km west of Vya, Washoe County, Nevada.

A male *M. c. princei* (H.J.E. No. 7) was among seven fleas collected 15 May 1963 from a spotted skunk (*Spilogale putorius gracilis* Merriam) that was trapped on Johnson Pass between the Stansbury and Onaqui Mountains in Tooele County, Utah (elev. 1830 m). This association was no doubt accidental. A second male (H.J.E. No. 6349) was the only flea from a sagebrush vole trapped 13 February 1969 about .4 km west of the previous locality.

Both traplines were set among rock outcrops and ledges on dry hillsides where the dominant plants were sagebrush (*Artemesia* sp.) and juniper trees (*Juniperus osteosperma* (Torr.) Little). Other small mammals commonly collected there were the deer mouse (*Peromyscus maniculatus sonoriensis* (Le Conte)), canyon mouse (*P. crinitus pergracilis* Goldman), long-tailed vole (*Microtus longicaudus latus* Hall), desert wood rat (*Neotoma lepida lepida* Thomas), bushy-tailed wood rat (*N. cinerea acraia* (Elliot)), cliff chipmunk (*Eutamias dorsalis utahensis* Merriam), and Great Basin pocket mouse (*Perognathus parvus olivaceus* Merriam). Despite several efforts to capture them in both livetraps and snaptraps, sagebrush voles were rarely trapped here or at numerous other places in the Bonneville Basin where conditions seemed more favorable.

The two specimens of *M. c. princei* were originally misidentified by me as atypical *Megabothris abantis* Rothschild. At the time, this was the only species of *Megabothris* known from Utah (Stark 1958), and I was unfamiliar with *M. clantoni*. The discovery of my error made me realize that the range of *M. abantis* within the Bonneville Basin was limited to the Oquirrh Mountains. In the Oquirrh Mountains *M. abantis* was the most common flea on western jumping mice (*Zapus princeps utahensis* Hall), but was also found regularly inripparian situations and on adjacent damp hillsides above 1525 m on long-tailed voles, and less commonly in the same location on deer mice associated with *Zapus*. In years of collecting in suitable habitats, scientists have failed to trap jumping mice in other mountains within the Basin; *M. abantis* was not found among hundreds of fleas collected from long-tailed and montane voles, deer mice, and other small mammals in the West Tintics, Stansburys, Onaquis, Sheeprocks, and other western Utah mountains. Stark believed the preferred hosts of *M. abantis* in Utah were microtines. If this is so, I have no reasonable explanation for the restricted range of *M. abantis* in an area where *Microtus* are common and widely distributed. My evidence strongly suggests that the presence of this flea in the Bonneville Basin is dependent on the occurrence of jumping mice. Past climatic and ecological changes of the Pleistocene Epoch must explain the disjunct distribution of *Z. princeps* and other essentially montane mammals in this part of Utah. Conditions in the Pleistocene Epoch apparently enabled certain small mammals to penetrate further west from the centrally located Wasatch cordillera than did other small mammals. The habitat that permitted this differential expansion no longer exists, and the distribution of some species was fragmented into scattered populations confined to higher elevations. (See Durrant 1952 for further discussion of the influence of Pleistocene Lake Bonneville on the distribution and speciation of mammals.)

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I never trapped *Lagurus* in the Oquirrh Mountains, and I know of no fleas being saved from sagebrush voles collected there. Durrant (1952) reported collecting specimens of *L. c. intermedius* from a locality on the east side of the Oquirrh Mountains in Salt Lake County, and there is reason to believe that *M. c. princei* and *A. sibirica* will eventually be found there.

I collected *M. abantis* from *Z. princeps* and *M. clantoni* ssp. from *L. curtatus*; the specimens were trapped within 10 yards of each other in southeastern Oregon.

Thrassis bacchi johnsoni Hubbard is the only known *Lagurus* flea that has not been found in Utah. Two specimens of *Thrassis* that I found on a sagebrush vole collected in Uinta County, Wyoming, a few miles from the Utah-Wyoming boundary were identified by Stark as *Thrassis bacchi caducus* (Jordan). Because of their implication in plague elsewhere (Hubbard 1949 and others), all of Utah's *Lagurus* fleas should be added to Allred's (1952) Utah list of plague-important fleas.

Assistance from two former associates, J. G. Bittmenn and J. A. Petrovich, is recognized with thanks. Suggestions for improving the manuscript were made by D. M. Allred, C. D. Jorgensen, H. E. Stark, and V. J. Tipton. Most mammal names are according to Durrant (1952). This work was accomplished in part while I was a research mammalogist at the University of Utah.

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INTERPOPULATIONAL VARIATION OF BLOOD PROTEINS IN PIKA (*OCHOTONA PRINCEPS SAXATILIS*)

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Abstract.— Studies were undertaken to examine the degree of divergence in four populations of pika in Colorado. Separation of blood proteins was accomplished utilizing acrylamide-gel disc electrophoresis. Separate analyses of variance were carried out for the relative mobilities of two of the transferrins (designated RMβ_1 and RMβ_2), the mean relative distance difference of the two tranferrins (DM), and the density of the most prominent albumin (α_1) and transferrin (β_2) bands. Although the four populations were characterized by a general similarity of the gel patterns, both interpopulational and sexual variations were observed. Variations between the sexes had to do with the amounts of protein, not with differences in protein mobility. The only significant populational differences were found in reference to density and DM. The interpopulational differences may serve as an indicator of populational divergence that has not been indicated by standard morphological characters. The significant patterns of variation observed in the blood proteins of the four populations studied may reflect a lack of gene flow between isolated populations.

North American pika are boreal mammals that occur in "island" populations on mountains throughout much of western North America. Pika are restricted to a narrowly defined habitat (the talus zone), and movement between neighboring populations is likely to be quite limited. Smith (1974) has estimated, for example, that distances greater than 300 m appeared to pose difficult barriers to dispersing juveniles.

The extent of genetic isolation among different populations is largely unknown, and studies aimed at determining geographic variation in pika are necessary. The subspecies of *Ochotona princeps* were revised by Howell (1924), and a synopsis is provided by Hall (1951). A total of 35 subspecies are currently recognized. The subspecies do differ in their cranial dimensions, but previous reports have indicated that there is little divergence in pika populations on the basis of size morphology.

The present study was designed to examine variations in blood proteins in four populations of *Ochotona princeps saxatilis* in Colorado.

The interpretation of electrophoretic mobility of various blood constituents as a means of discovering differences between separate populations has received much discussion and criticism over the past few years. However, the fact that most of these substances are partly protein, thus bearing a close translational relationship to the gene itself, points up at least hypothetically the value of such investigations.

Methods

Collecting Localities: A total of 41 pika were collected from four localities in Colorado. The areas were Evans and Goliath in Clear Creek County, Audubon in Boulder County, and Crown Point in Larimer County. The ranges of elevations over which animals were collected at each site were 3,902–4,085 m, 3,537–3,659 m, 3,598–3,841 m, and 3,354–3,506 m, respectively.

Blood Samples: Animals were shot and blood was withdrawn from the heart usually within three minutes. Heparinized 1.4–1.6 mm micro-hematocrit capillary tubes were filled to within one-half inch of one end, and were subsequently made airtight at both ends with plastic Crito-caps. All sealed hematocrit tubes were placed in glass vials, packed in snow, and shielded from sunlight during transport to the laboratory. Immediately upon arrival in the laboratory, hematocrit tubes were centrifuged at 11,500 rpm using an IEC microcapillary centrifuge. The tubes were broken at the cell-plasma interface, and the plasma was frozen until electrophoretic determinations were made.

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Electrophoresis: Electrophoresis of plasma proteins from 41 animals was accomplished using the acrylamide-gel disc technique (7 percent acrylamide) described by Smith (1968).

The electrophoretic chamber (Buchler Instruments) held a total of 12 gel tubes. Current was applied initially for 12 minutes at 1.5 milli-amps/gel in a tris-glycine buffer at pH 9.5. Following this initial warm-up period, gels were run at 4.0 milli-amps/gel for 30 minutes. A gelman six-volt power source was used for all separations. No spacer or sample gel was employed, and 20 μl of plasma was mixed with 40 μl of 50 percent sucrose and was placed directly on the running gel. Tubes containing purified bovine albumin were run as controls.

Following separation, gels were stained for 45 minutes in analine blue-black. Destaining required approximately five days and was accomplished in a series of three 7 percent acetic acid baths. Whole gels were analyzed densitometrically using a Densicord recording electrophoresis densitometer (Photovolt Corporation). An integrater (Integraph Model 49) automatically measured the areas under the densitometric curves. Analysis of densitometric curves followed the procedures outlined by Dalby and Lillevic (1969).

RESULTS AND DISCUSSION

Table 1 summarizes mean values resulting from measurements of densitometric tracings of the stained acrylamide gels. Because no tests were run to confirm the chemical identity of the protein bands, RMβ_1 and RMβ_2 refer only to relative mobilities of what are presumed to be the same two bands in the transferrin range. Likewise, α_1 and β_1 are measurements of the height of the densitometric curve of the most prominent presumed albumin and transferrin band respectively. The parameter DM represents

$$\frac{\Sigma(\mathrm{RM}\beta_2-\mathrm{RM}\beta_1)}{n}$$

for each of the eight sample groups investigated.

Analyses of variance were run on RMβ_1, RMβ_2, albumin and transferrin heights, and the mean relative distance (DM). Patterns of statistically valid sexual variation were seen in regard to the height of both the α and β bands; sexual differences in RMβ_1, RMβ_2, and DM were not significant. Statistically significant differences among geographical collecting areas were found only in reference to β_1 height and DM. None of

TABLE 1. Electrophoretic data: Means ± Standard Deviations.

Area	Sex	Sample Size	RMβ_1	RMβ_2	a_1	β_1	DM
Evans	Males	5	0.569 ± 0.004	0.717 ± 0.005	21.800 ± 0.447	10.000 ± 2.121	0.147 ± 0.001
Evans	Females	10	0.575 ± 0.015	0.718 ± 0.014	21.700 ± 0.483	10.300 ± 2.907	0.143 ± 0.010
Audubon	Males	6	0.576 ± 0.006	0.698 ± 0.006	21.166 ± 0.408	6.166 ± 1.602	0.122 ± 0.003
Audubon	Females	3	0.575 ± 0.007	0.716 ± 0.003	21.666 ± 0.577	7.333 ± 1.154	0.140 ± 0.005
Goliath	Males	3	0.569 ± 0.010	0.717 ± 0.008	21.666 ± 0.577	7.666 ± 0.577	0.148 ± 0.002
Goliath	Females	7	0.568 ± 0.007	0.721 ± 0.011	21.857 ± 0.377	11.285 ± 3.039	0.153 ± 0.008
Crown	Males	4	0.565 ± 0.006	0.704 ± 0.024	21.000 ± 0.816	5.750 ± 1.500	0.139 ± 0.023
Crown	Females	3	0.569 ± 0.006	0.702 ± 0.039	22.000 ± 0.000	8.666 ± 1.527	0.132 ± 0.036

the Area X sex interactions were significant.

The main objective in regard to examination of patterns of electrophoretic plasma protein migration was to uncover possible interpopulational variations of a striking nature. If these variations were to exist, they perhaps might be an indication of a stable phenotypic characteristic, which, when viewed with phenotypic characters of a morphological type, might indicate a high or low degree of populational divergence.

That this divergence might be expected is based on the relative altitudinal isolation of pika populations in Colorado. The fact that high talus regions are generally separated by non-talus areas and the general reluctance of the pika to leave the talus habitat seems to preclude the necessity of distance as a block to gene flow. This does not mean to suggest that gene flow is the salient factor causing population divergence. It is possible that even in the absence of continued gene exchange, these animals have evolved in parallel fashion due to the relative similarity of selective pressures.

Crown Point and Mount Audubon are widely separated from each other as well as from Mount Evans and Mount Goliath. There would seem, in these instances, to be a reduced amount of reproductive activity between populations. Because they are separated by a distance of only about five miles, Evans and Goliath might be treated as a single population. It is possible, however, that gene flow even between these two areas has been minimal or non-existent.

Although divergence of three of these populations might be expected on the basis of restricted gene exchange, the present classifications of North American pikas are based entirely on morphological characters which, with the exception of pelage color, seem to show little variation (Broadbooks 1965). It was deemed worthwhile, then, to examine plasma protein migration patterns as a more precise indication of possible populational differences.

In interpreting any variation found in a study of this nature, one must resist the urge to attribute them all to stable genotypic characteristics. Indeed, more information is needed from breeding experiments and from expanded analysis of individual protein components before a more confident stand can be taken in regard to the genotypic stability of a difference. There is no question that the literature warns against over-zealous interpretation of any measured protein variations. It might be prudent, therefore, to approach interpretation of data of this type from the standpoint of similarities in migration patterns.

Although patterns of both interpopulational and sexual variation are present, there is a general similarity of the gel patterns from the four areas. In addition to the obvious height differences in some curves, the presence of a dense band very close to the origin in some samples from both sexes from Mount Evans and from Mount Goliath are the most noticeable differences in an otherwise generally common pattern.

The presence of significant sexual variation is not surprising, as was pointed out by Moore (1945). Female animals do seem to have denser β_1 and α_1 bands than do males. It is interesting that there seem to be differences only in the amount of a protein rather than the type of protein molecule, as there were no significant patterns of variation in protein mobility between sexes. The significant pattern of variation between locations in regard to the β_1 band is probably due to bias introduced by the larger number of female samples from some locations.

The significant differences in DM between geographic areas seem to indicate differential migration rates of the entire samples. The DM is, in fact, a measure of the overall linear variation in both the gels (and consequently the tracings), and it is precisely why the tracings do not superimpose exactly. These interpopulational differences seem to be real. That they are stable genetic characters cannot be determined from this analysis; they may, however, be an indicator of population divergence that cannot be measured in terms of standard morphological characters.

Although interpretation of electrophoretic plasma protein migration patterns should be approached with caution, such interpretation has the potential of uncovering more subtle differences that may not be mirrored in standard taxonomic characters. At this point, one can only say that the significant patterns of variation found in regard to plasma protein mobility may support the possibility of a predicted lack of gene flow between isolated populations of pika.

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OBSERVATIONS ON THE DISTRIBUTION OF MICROORGANISMS IN DESERT SOIL

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Abstract.— Population estimates of fungi, bacteria, and actinomycetes in desert soil were determined with respect to soil depth and distance from shrubs. In general the highest numbers of microbes were found at the shrub base; the lowest numbers were found in the interspaces. While the total number of organisms usually declined in deeper soil, the relative importance of the actinomycetes increased. These population trends are attributed to substrate availability and utilization and interspecific interactions.

As the soils became drier and warmer the total number of microorganisms decreased. Mold populations remained at about the same level during the study. While the numbers of both bacteria and actinomycetes declined, the relative importance of the actinomycetes increased.

The numbers and activities of soil microflora are important in desert soils in the processes of root and litter decomposition, for the timing and release of nutrients tied up in dead organic matter, and also for the physical binding of soil particles (Went and Stark 1968, Khudairi 1969, Fuller 1974). For this report we determined spatial and temporal differences in the populations of fungi, bacteria, and actinomycetes in Mojave Desert soils.

This work was conducted as part of a large study of primary productivity and nutrient interrelationships sponsored by the U.S. International Biological Program (IBP). Soils were gathered from the IBP Desert Biome's Rock Valley validation site, Nye County, Nevada. This area is in the northern Mojave Desert about 100 km northwest of Las Vegas, and is part of the U.S. Energy Research and Development Administration's Nevada Test Site. In Rock Valley soils are well-drained and have moderate permeability. Soil beneath shrubs is fine sand to depths of around 15 cm, gravelly loamy sand to 33 cm, and cemented gravel between 33 and 57 cm. Soils in bare areas are gravelly sandy loam to around 43 cm, and cemented gravel below that (Romney et al. 1973). The vegetation is composed primarily of perennial shrubs, which cover about 20 percent of the surface. More detailed descriptions of edaphic and biotic features may be found in Turner (1974).

Methods

Soil was sampled from nine locations during the middle of the plant growing season, March-April 1973, around the shrub species, *Lycium andersonii* Gray. Samples were collected from three depths (0–10 cm, 10–20 cm, and 20–30 cm) at each of three distances from the shrub: the shrub base (samples 1, 2, and 3, starting at the surface), at the canopy edge or one shrub radius (samples 4, 5, and 6), and in the shrub interspace or three-canopy radii from the plant base (samples 7, 8, and 9). These soil samples were aliquots of those used in other below-ground studies of root biomass and soil ATP activity (Bamberg et al. 1974).

Dilution plate counts were made to quantify and differentiate the fungal and bacterial populations of the soil samples collected during the 12th, 13th, 15th, and 16th weeks of 1973. Twenty grams of oven-dried soil (ODS) from each soil sample were added to

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100 ml of sterile, distilled water and were shaken for 10 minutes. Coarser particles were allowed to settle, and one-ml samples of the soil suspension were used to prepare dilutions for plate counts according to standard procedures (Clark 1965). The dilutions used were $5X10^{-2}$ and $5X10^{-3}$ for fungi and $5X10^{-4}$ and $5X10^{-5}$ for bacteria-actinomycete counts. Five plates of each dilution were poured. Cooke's Rose Bengal agar with 35 μg Aureomycin/ml added was used for fungal determinations, and sodium albuminate agar was used for bacteria and actinomycetes. The plates were incubated at room temperatures. Mold counts were made after two days, and bacteria and actinomycetes were counted after 14 days.

Penicillium, *Aspergillus*, and *Streptomyces* were differentiated and their percents of occurrence were reported.

Soil pH was measured using a 1:5 soil solution. Determinations of soil moisture were made after the soil was oven-dried at 105–110 C for 24 hours. Total numbers of organisms per gram of oven-dried soil were calculated according to the method of Clark (1965).

Root biomass was determined by a combination of sieving and flotation in saturated $MgSO_4$ solution (see Bamberg et al. 1974).

RESULTS

Soil pH averaged about 9.0 and did not vary significantly with either location or time. Soil temperature and moisture are presented in Table 1.

Temperatures, which were taken in the morning, showed little variation within a sampling period with the exception of Location 7. As one might expect, this surface sample in the interspace was slightly warmer than soil from the other locations. Soil temperatures for April during the 15th and 16th weeks averaged 5-10 C higher than those from March.

At the shrub base and the canopy edge the soil moisture decreased from about 15 percent during weeks 12 and 13 to about 5 percent during weeks 15 and 16. With the exception of week 13, little change in soil moisture was noticed over this period of time at the interspace locations. The high moisture levels for week 13 were the result of 25 mm of rain that fell during the period between the first and second sampling dates. Moisture content in the interspace was slightly lower at week 12 and higher at week 16 than in the other locations.

There was considerable variation in root biomass under *Lycium andersonii* during the study (Table 2). Most of the roots (64 percent) were found under the shrub and the least (less than 7 percent) were present in the interspaces. Root biomass at the shrub base usually decreased with depth, while vertical distribution was fairly uniform at the canopy edge and in the interspaces. Flowering and continued growth occurred during the sampling period; fruit formation had started by the end of this period.

Estimates of the population sizes of fungi, bacteria, and actinomycetes are given in Table 3 for soil samples collected between the 12th and 16th weeks of 1973 from Rock Valley. Table 4 and Figure 1 show the percentage of the total mold population made up of organisms of the genera *Penicillium* and *Aspergillus*. Over 95 percent of the actinomycetes isolated belonged to the genus *Streptomyces*.

Results are summarized according to location:

1. Shrub Base: At the plant base the mold numbers in the surface soil increased during the course of the study. As the spring progressed the number of fungi decreased by about half at the 20–30 cm level. *Penicillium* was the dominant fungal genus underneath the shrub throughout the five-week period. The relative importance of *Aspergillus* dropped off during weeks 15 and 16.

Populations of bacteria and actinomycetes were much higher than those of the fungi. In April the numbers of bacteria decreased by 55–85 percent. During the study *Streptomyces* increased its dominance under the shrub from 50 percent to 80 percent, even though actual numbers declined. Bacterial population size estimates did not appear to be related to sample depth.

2. Canopy Edge: Soil from the canopy edge taken at locations 4, 5, and 6 yielded mold population estimates that did not

change radically during the experiment. Soil from Location 6 usually yielded a lower number of fungi than did soil from shallower depths. *Penicillium* dominance over *Aspergillus* increased sharply during weeks 15 and 16.

Bacteria and actinomycete numbers were lower at the canopy edge than they were underneath the shrub. Population size and dominance trends of these two groups followed those found at the plant base.

3. Interspaces: The lowest total numbers of fungi were found in the shrub interspace. Mold counts in April were highest at the 0–10 cm level. In the shrub interspaces, *Aspergillus* replaced *Penicillium* as the dominant genus.

The populations of bacteria and actinomycetes at three canopy radii from the shrub base were slightly lower than those at the canopy edge. With the exception of week 13, there was little difference in population size estimates with time or depth. *Streptomyces* continued its strong dominant role.

DISCUSSION

Generally both root biomass and total number of microbes were highest at the shrub base. This relationship indicates that the soil microflora utilize the roots or root exudates as a substrate (Starkey 1958, Friedman and Galun 1974). It must be pointed out, however, that other types of organic matter, such as litter, had a distribution pat-

TABLE 1. Soil temperature and moisture at nine sample locations during March and April 1973.

	Sample Location								
Week	Shrub Base			Canopy Edge			Interspace		
	1	2	3	4	5	6	7	8	9
Temperature (C)									
12	8.5	9.0	9.5	9.0	9.0	9.5	10.0	9.0	8.5
13	8.5	9.0	10.0	9.0	9.0	10.0	10.9	9.0	9.0
15	18.0	16.5	16.0	17.0	15.0	15.0	24.0	18.0	16.0
16	14.5	12.5	13.0	13.0	12.0	13.0	16.0	15.0	13.0
Moisture (%)									
12	15	15	16	14	15	15	9	10	13
13	14	16	17	16	19	17	17	19	17
15	5	6	6	5	6	6	7	7	7
16	5		6	3	5	7	7	10	13

TABLE 2. Root biomass (gODW/1 soil) in relation to sample location under *Lycium andersonii* in Rock Valley, 1973.

	Sample Location								
Week	Shrub Base			Canopy Edge			Interspace		
	1	2	3	4	5	6	7	8	9
12	5.5	2.9	2.8	1.1	6.3	1.7	<0.4	<0.6	<0.4
13	1.4	8.9	1.5	6.0	1.6	2.6	<0.3	<0.2	<0.3
15	3.9	2.1	2.9	1.5	1.6	0.4	1.4	0.5	0.3
16	14.9	8.8	10.3	1.7	1.1	5.2	<0.3	0.3	1.9

tern similar to that of roots (Bamberg et al. 1974).

Fungal populations remained relatively stable as the season progressed. Bacteria and actinomycetes, however, decreased with time. These changes in the microbial community are probably related to soil moisture. Soil water potentials reached about –25 bars in April in Rock Valley. Bacterial activity is known to decline rapidly when the soil water potential drops below –5 bars, while many fungi and actinomycetes can tolerate much lower water potentials (Griffin 1972). Increases in the relative importance of streptomycetes and fungi may be partially attributable to reduced competition by bacteria. The percent of *Streptomyces* increased in April, which may indicate the beginning of a more active decomposition role assumed by this group. This increase is particularly evident at the shrub base and canopy edge.

Penicillium was the dominant mold genus close to the plant, but *Aspergillus* was also common in the surface soils and was dominant in the interspace zone. Since these two genera are spore-formers, plate counts may only indicate the potential rather than the actual activity during the sampling period. The sample locations at which *Aspergillus* numbers were highest are also those that usually become the warmest and driest during the year. These results agree with reports that have found *Aspergillus* to be a more xerothermic genus than *Penicillium* (Griffin 1972).

As mentioned previously, roots, root exudates, and other substrate matter influence the soil microflora. Mold populations were found to decline in deeper soil, while *Streptomyces* dominance increased with soil depth. These differences may have resulted because the availability of preferred nutrient sources varied with soil depth. Most of the roots were located in the upper 20 cm of the soil. Siu (1951) reported that actinomycetes were generally poor cellulose utilizers, while fungi were highly cellulolytic. Went and Stark (1968) postulated that fungi may play an important role in deserts not only in decomposition of soil organic matter but also in the direct cycling of nutrients to living roots from dead organic material.

TABLE 3. Plate counts from soil gathered at nine locations during March and April 1973 (Organisms /gODS).

	Sample Location								
Week	Shrub Base			Canopy Edge			Interspace		
	1	2	3	4	5	6	7	8	9
	Fungi $X10^3$								
12	25.5	24.9	30.8	23.0	24.5	8.5	9.9	13.1	3.9
13	41.4	22.4	26.1	9.3	23.0	9.8	3.8	3.4	9.2
15	44.7	50.3	16.3	20.1	23.5	12.7	13.2	9.0	5.2
16	47.8	27.8	16.8	18.3	15.1	10.3	7.3	3.6	4.7
	Bacteria $X10^5$								
12	34.4	93.0	78.8	26.6	63.7	13.6	9.6	13.8	3.3
13	82.2	54.4	20.8	34.3	22.3	22.3	23.1	38.0	16.6
15	5.8	16.9	4.6	11.8	9.4	11.5	18.4	10.7	13.3
16	15.6	19.9	10.4	7.0	9.9	6.8	17.3	4.8	5.9
	Actinomycetes $X10^5$								
12	51.6	73.0	67.2	45.4	66.3	54.4	19.4	29.2	33.7
13	72.9	92.6	78.2	53.7	70.7	74.7	53.9	72.0	66.4
15	39.2	48.1	18.4	35.3	29.6	25.5	35.6	26.3	24.7
16	36.4	63.1	58.7	30.0	33.1	38.3	16.7	25.2	21.1

Table 4. Percentage of total mold colonies composed of the genera *Penicillium* and *Aspergillus*.

	Sample Location								
Week	Shrub Base			Canopy Edge			Interspace		
	1	2	3	4	5	6	7	8	9
	Penicillium								
12	17	54	93	23	48	40	6	21	13
13	35	50	32	21	60	16	0	15	7
15	71	72	58	50	50	29	14	19	29
16	73	25	36	44	75	56	3	6	4
	Aspergillus								
12	13	15	4	10	42	12	62	61	10
13	27	13	8	27	17	16	47	71	1
15	2	3	3	4	4	2	78	57	64
16	1	6	21	8	9	22	71	39	19

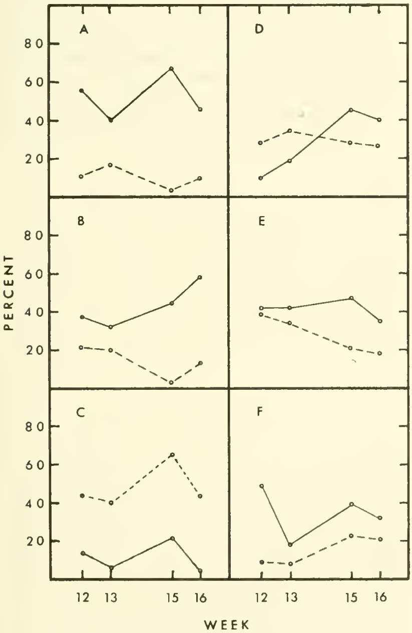

Fig. 1. Percentage of all fungi represented by the genera *Penicillium* (solid line) and *Aspergillus* (dashed line) at: A. Shrub Base (locations 1, 2, and 3); B. Canopy Edge (4, 5, 6); C. Interspace (7, 8, 9); D. 0-10 cm (1, 4, 7); E. 10-20 cm (2, 5, 8); F. 20-30 cm (3, 6, 9).

Alexander (1971) stated that the extant conditions in a habitat will dictate that only one, or a few, of the indigenous species will actually exploit an energy source. The fact that seasonal variation in the soil environment will cause a shift in the relative numbers of various microbial populations is seen by the higher percentage of *Streptomyces* in week 16 over week 12 at the shrub base location. This response corresponds with a decrease in moisture and an increase in temperature during that time interval. The numerical dominance of *Streptomyces* in this study may be attributable to the warm, dry nature of our desert soils.

Throughout the sampling period actinomycetes outnumbered bacteria; fungi represented only a small portion of the total number of microorganisms. These results agree with those reported for other desert soils (Fuller 1974). It has been pointed out, however, that enumeration techniques alone do not necessarily give an accurate indication of the importance of the various microbial groups. For example, while these methods usually give low population estimates for molds, fungal biomass often exceeds that of other microorganisms (Went and Stark 1968, Fuller 1974).

We feel, however, that differences in the number of observed colonies within the various groups of microorganisms are good indicators of spatial and temporal fluctuations in population size. These population trends in turn give an indication of changes in the relative importance of the different microbial groups.

ACKNOWLEDGMENTS

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HOME RANGE OF THE WESTERN JUMPING MOUSE, *ZAPUS PRINCEPS*, IN THE COLORADO ROCKY MOUNTAINS

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Abstract.— Western jumping mice, *Zapus princeps*, were live-trapped during the summer of 1975 in an aspen forest in the Front Range of the Colorado Rocky Mountains. Home range sizes were calculated using the exclusive boundary strip method, and it was discovered that males had larger home ranges (298–3315 m^2, $\bar{x}$ = 1743 m^2) than females (680–1275 m^2, $\bar{x}$ = 1041 m^2). Mean range length was 96.5 m for males and 78.5 m for females. Spatial relationships showed that females tended to be more territorial than males, based on the females' higher percentage of exclusive home ranges, greater distance between centers of activity, and more uniform spacing.

Jumping mice (Zapodidae) are widely distributed over North America. The two eastern species (*Zapus hudsonius* and *Napaeozapus insignis*) have been the subject of considerable research (e.g. Snyder 1924; Sheldon 1934, 1938a, 1938b; Hamilton 1935; Blair 1940; Quimby 1951; and Whitaker 1963a, 1963b). However, ecological literature on the western jumping mouse (*Zapus princeps*) is sparse. Krutzsch (1954) briefly discussed the natural history of *Z. princeps* in the Rocky Mountains, and Brown (1967a, 1970) has provided information on its reproductive and seasonal activity patterns. Although information is available on habitat selection by *Z. princeps* (Brown 1967b, Clark 1971, Armstrong 1972), little is known of their spatial patterns within a single habitat type. Analysis of these spatial patterns was the thrust of the present study.

Materials and Methods

The study was conducted in an aspen forest adjacent to the University of Colorado Mountain Research Station, Nederland, Colorado, at an elevation of approximately 2900 m. This forest was mesic and willow (*Salix*); monkshood (*Aconitum columbianum*), cowparsnip (*Heracleum lanatum*), Canadian reed grass (*Calamagrostis canadensis*), and bluegrass (*Poa* spp.) dominated the understory.

The study area consisted of an 8 x 10 grid of trapping stations spaced 10 m apart. Three small Sherman live traps were placed at each station. The study area was sampled for four days twice a month during July, August, and September 1975. On capture, each individual was sexed, weighed, marked by toe-clipping, and then released. Location of capture for each individual was also recorded.

The exclusive boundary strip method was used to measure home range size. The external points of capture are connected, and the resultant area is considered the home range of the individual. Centers of activity were calculated using Hayne's method (1949) and were used to assess nearest neighbor distance (Clark and Evans 1954).

Results

A total of 58 individuals was captured during the summer of 1975 in 5760 trap-nights, representing an average monthly density of 31.0/ha (range 28.0–35.0). This density was extremely high compared to values obtained by Brown (1970), whose population densities averaged 3.2/ha over a four-year period. Population numbers were stable on a monthly basis, probably due to the high longevity characteristic of *Zapus* (Quimby 1951, Brown 1970).

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All animals captured five or more times were used in the calculation of home range size ($N = 37$). The average home range size of males was 1743 m^2 (298–3315 m^2), and that of females was 1041 m^2 (680–1275 m^2). The mean range length (greatest distance between captures) was 96.5 m for males and 78.5 m for females. These differences between the sexes were highly significant ($p < .01$, t-test). Brown (1970) obtained mean range length values twice the present values (210.0 m and 155.0 m respectively), but this is because the population of *Zapus princeps* that he studied showed an extremely narrow, elongated distribution along a mountain stream.

DISCUSSION

Home Range Size

Home range, as applied to mammals, has been defined by Burt (1943) as "the area transversed by the individual in its normal activities of food gathering, mating, and caring for young." Home range values for *Zapus princeps* in this study were considerably lower than those found by Myers (1969). Myers obtained home range values of 3075 m^2 for males and 2350 m^2 for females. There are several possible reasons for the discrepancy: (1) track- versus trap-revealed home ranges, (2) different population densities, and (3) differences in vegetation structure of the habitat. Myers used the tracking method of Justice (1961) to monitor animal movements, and the results of track- versus trap-revealed home ranges do not seem to be directly comparable. Metzgar (1973) found that track-revealed home ranges were larger than trap-revealed home ranges.

Myers captured a total of 25 *Zapus princeps* throughout the whole summer on a 1.1 hectare plot, whereas in the present study the average monthly density was 31.0/hectare. It has been well documented that home range size varies inversely with population density (Burt 1943, Getz 1961, Van Vleck 1969, Mazuriewicz 1971, and Maza et al. 1973).

Also, Myers does not describe the habitat's vegetation structure, which may influence home range size. In the present study, the aspen forest was very productive, and Kenagy (1973) proposed that in years of high resource levels animals forage over smaller areas since in the smaller areas food is readily available and less energy expenditure is required for foraging. And O'Farrell et al. (1975) point out that home ranges of *Perognathus parvus* were affected jointly by resource levels and population size; neither of these factors acted independently.

The exact reason for the large difference in calculated home range sizes is not known, but home range size is quite labile and many factors, both intrinsic (e.g. population size) and environmental, influence its size.

The home range size of *Zapus princeps* is similar to that of the meadow jumping mouse, *Z. hudsonius*, in Minnesota. Quimby (1951) used the inclusive boundary strip method, where the external points of capture are considered centers of rectangles whose boundaries are half the distance to the next trapping station, to determine home range size in *Z. hudsonius*. To facilitate comparison with the present study, Quimby's values were reduced 15 percent (see Stickel 1954); this reduction results in home range sizes of 1479 m^2 for males and 1307 m^2 for females. The similarity in home range size is not surprising, since Quimby (1951) found that the preferred habitat of *Z. hudsonius* in Minnesota was willow thickets—and the understory of the aspen forest in the present study was dominated by willows.

McNab (1963) proposed that "hunters" (carnivores, insectivores, and granivores) require a larger home range than "croppers" (herbivores). The home range size of two other species of rodents (*Microtus longicaudus* and *M. montanus*) found in the area were calculated using the same method. *Zapus princeps* is a primary granivore, with seeds of the graminoids being most important, while members of the genus *Microtus* are primary herbivores (Lechleitner 1969, Clark 1971). The average home range of *Z. princeps* was significantly larger ($p <$

.001, t-test) than that of the microtines (Table 1). The rationale for the difference in home range size is that food resources of hunters show a more dispersed distribution than that of croppers, and therefore must travel farther on foraging trips.

TABLE 1.— Home range size of three species of rodents.

		Home Range Size		Range Length	
Species	N	Male	Female	Male	Female
Microtus longicaudus	11	485 m^2	364 m^2	42.0 m	30.5 m
Microtus montanus	4	283 m^2	—	25.0 m	—
Zapus princeps	37	1741 m^2	1012 m^2	96.5 m	78.5 m

Territoriality

Getz (1961) suggested that territoriality can be inferred from five criteria: (1) percentage of exclusive (non-overlapping) home ranges between members of the same sex, (2) percentage of at least partially exclusive home ranges between members of the same sex, (3) distance between centers of activity, (4) distribution of centers of activity, and (5) sex of individuals involved in multiple captures. In this study 71 percent of the males had inclusive home ranges, while no females had inclusive home ranges. Both males and females had home ranges that were partially exclusive (29 percent and 84 percent respectively). Sixteen percent of the female home ranges were totally exclusive.

Centers of activity were calculated according to the method of Hayne (1949). The average distance between centers of activity was 11.1 m for males and 15.3 m for females. This difference in mean distance between centers of activity was significant ($p < .01$, t-test).

Getz (1961) hypothesized that if the sex ratio of the population is equal and if territorial behavior is not displayed, then the nearest neighbor should be of the same sex at least half the time. In this study, the nearest neighbor was always the opposite sex. Hanson and Fleharty (1974) believed this indicated that territorial behavior was exhibited by both sexes, but there may be an alternative explanation. In some rodent species mated pairs often share the same nest or nest in close proximity, and this may be the case with *Zapus princeps*. The fact that the nearest neighbor is of the opposite sex may just be a by-product of this reproductive behavior, and not a by-product of territorial behavior.

The distribution of centers of activity should approach uniformity if territorial behavior is displayed (Getz 1961). Clark and Evans (1954) established "R" as the ratio of the observed mean distance to nearest neighbor to the expected mean distance to nearest neighbor in an infinitely large random distribution. R has a finite range, with values indicative of perfectly clumped (0.00), random (1.00), and uniform (2.1491). Distributions of *Zapus princeps* based on centers of activity showed that both sexes tended towards uniform spacing ($R = 1.33$ for males and 1.51 for females). This difference between the sexes was significant ($F = 3.455$, $p < .01$).

There were no multiple captures of *Zapus princeps* in the present study. Quimby (1951) indicated that *Z. hudsonius* was a solitary feeder, and multiple captures were rare. The same may be true with *Z. princeps*.

The analysis of spatial relationships suggests that males are quite tolerant to each other (71 percent of home ranges inclusive), and that females tend to be more territorial than males, based on their higher percentage of exclusive home ranges, greater distance between centers of activity, and more uniform spacing.

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PRELIMINARY MAMMAL SURVEY OF FOSSIL BUTTE NATIONAL MONUMENT, WYOMING

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Abstract.— The mammalian community of Fossil Butte National Monument, Wyoming, consisted of at least 45 species. Snap trap sampling of the smaller species combined with sight and sign observations of the larger species formed the basis of this preliminary survey in the summers of 1974 and 1975. Snap-trapping samples (2880 trap days) yielded 44 least chipmunks and 89 deer mice. The distribution of all species was characterized by plant community occupancy. Heavy domestic livestock use of the communities nearest water has resulted in severe alteration in community structure; this has probably affected the distribution and abundance of at least some of the smaller mammals.

Fossil Butte National Monument, world famous for its ichthyological fossils, is a recent addition (1973) to the National Park System; it is about 18 km west of Kemmerer, Lincoln County, Wyoming. A preliminary survey of the mammals of the monument was made in the summers of 1974 and 1975 and may serve to develop public understanding and appreciation of the fauna and to promote more comprehensive ecological investigations.

Study Area

Fossil Butte (3313 m above sea level) is a ruggedly impressive topographic feature rising from 2272 m at base. The climate is semiarid and cool-temperate. Annual precipitation, most of which falls as snow, averages about 23 cm. Winters are cold; summer days are warm, but summer nights are cool.

The monument lies in the Rocky Mountain Faunal Area (Long 1965). However, the Idahoan and Upper Green River divisions of the faunal area meet in the general area of the monument, bringing several species groups into contact. Six major plant communities, indentified on the basis of physiognomy and taxonomy of the predominant overstory vegetation, are described in Table 1. The vegetation of Fossil Butte was described previously by Beetle and Marlow (1974); they divided the area into 13 plant communities based on floral distribution. The correspondence of their communities to mine is listed in Table 1. Many of the communities listed by Beetle and Marlow (1974) are only a few meters wide and, as such, their boundaries were not meaningful to many mammalian species, especially the larger forms. Therefore, a lumping of their community categories seems necessary. Beetle and Marlow (1974) listed the species in each community. Vegetation of the monument appears characteristic of the surrounding area.

Methods

Methods depended on the species investigated. Ecological distribution of larger kinds (e.g., beaver, carnivores, ungulates) was determined by direct observation of animals or of their signs. Smaller mammals were sampled using snap traps. Snap-trap transects of 20 stations 15 m apart were placed in each plant community. Three traps were set at each station. Traps were baited with rolled oats and peanut butter and were checked in the mornings and evenings of four consecutive days.

Results

Twenty-three mammalian species were

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found on the monument, representing five orders, 11 families, and 22 genera. In addition, other unverified species no doubt occur on the monument.

Snap-trapping.— In 2880 trap days (TD) equally spaced among the six plant communities (Table 1), 134 small mammals were caught. The catch included only two species, the least chipmunk (*Eutamias minimus*) (N = 45) and the deer mouse (*Peromyscus maniculatus*) (N = 89). Both species were caught at relatively low rates (1.5 captures per 100 TD for chipmunks, and 3.1 captures per 100 TD for deer mice) when

TABLE 1. Comparison of plant communities occurring on Fossil Butte National Monument, Lincoln County, Wyoming.

Plant community	Corresponding plant communities identified by Beetle and Marlow (1974)	Prominent species	Life-form structure	Characteristics
Grass-Forb	(not listed separately)	Gramineae	Grasses, forbs	Occurs on more exposed areas, especially at higher elevations (Xeric)
Sagebrush-Grass	Alkali sagebrush and grass, Mt. big sagebrush and shrub complex, Mt. big sagebrush and grass complex, basin big sagebrush complex, shadscale saltbrush and shrub complex, shadscale saltbrush and alkalibrush complex, serviceberry complex	*Artemisia tridentata* Gramineae	Grasses, forbs, shrubs	Occurs on drier lowland sites (Xeric)
Mt. Mahogany	Mt. mahogany and serviceberry complex, Mt. mahogany complex, mixed shrub complex, chokecherry and antelope bitterbrush complex	*Cercocarpus montanus*	Grasses, forbs, shrubs	Occurs at higher elevations on flats and in protected areas on slopes (Xeric)
Pine	Mixed timber and shrub complex	*Pinus flexilis*	Grasses, forbs, shrubs, trees	Occurs on protected slopes, frequently on north-facing areas at higher elevations (Xeric-Mesic)
Meadow	(not listed separately)	Sedges (*Carex* sp.)	Grasses, forbs, sedges	Occurs in areas adjacent to willows and aspen on wet sites (Mesic-Hydric)
Aspen-willow	Aspen complex	*Populus tremuloides*; *Salix* sp.	Grasses, forbs, shrubs, trees	Occurs on wetter sites, usually on protected slopes, associated with springs and intermittent streams (Mesic-Hydric)

compared with capture rates for these species in studies 150 miles to the north (Clark 1975).

Capture rates of chipmunks increased from the Sagebrush-Grass (1.7/100 TD) and Aspen-Willow (1.7) communities to Mountain Mahogany (2.3) and Pine (3.7) communities. No chipmunks were caught in the two herbaceous communities of Meadow or Grass-Forb. Deer mice were present in all but the two wettest communities, Meadow and Aspen-Willow. They were least abundant in the Grass-Forb Community (1.8/100 TD), followed by Mountain Mahogany Community (2.8) and Sage-Grass Community (4.2), and were most abundant in the Pine Community (9.7).

Observations and signs.— Twenty-one other species or their signs were observed. Monument management philosophy and the author's time limitations precluded quantitative sampling of many larger forms.

Several species were distributed predominantly in the Grass-Forb and Sagebrush communities: desert cottontail (*Sylvilagus audubonii*), white-tailed jackrabbit (*Lepus townsendii*), Richardson ground squirrel (*Spermophilus richardsonii*), Uinta ground squirrel (*S. armatus*), and northern pocket gopher (*Thomomys talpoides*). Even though ground squirrels were abundant, none were captured. Three yellow-bellied marmots (*Marmota flaviventris*) were seen on the upper slopes. A single white-tailed prairie dog colony (*Cynomys leucurus*) of about 12 ha existed in Sec. 2, T21N, R118W; one sagebrush vole (*Lagurus curtatus*) was seen. Sixteen pronghorns (*Antilocarpa americana*), two badgers (*Taxidea taxus*), and a striped skunk (*Mephitis mephitis*) were sighted.

No species seemed to be restricted to the Mountain Mahogany Community, although nine mule deer (*Odocoileus hemionus*) and three elk (*Cervus canadensis*) were observed there. A moose (*Alces alces*) sign was evident in this community and two moose were seen in the Willow-Aspen Community. Red squirrels (*Tamiasciurus hudsonius*), bushy-tailed woodrats (*Neotoma cinerea*), and porcupines (*Erethizon dorsatum*) were associated mostly with the Pine Community. Two species were associated commonly with the Aspen-Willow Community; they were moose and beaver (*Castor canadensis*). Several *Microtus* species (i.e., *M. pennsylvanicus*, *M. montanus*, and *M. longicaudus*) expected in the Meadow Community were not found, nor were any runways or nests located (cf. Clark 1973). Long (1965) listed specimens of all three species collected within 25 km of the monument, which shows their general occupancy of southwestern Wyoming.

A few ubiquitous species were present, including coyotes (*Canis latrans*), long-tailed weasels (*Mustela frenata*), and wild horses (*Equus cabalis*) (N = 12).

Species of unverified presence.— Long (1965) listed 39 other species known to occur in the region. No evidence of their presence was found in this investigation.

Domestic livestock.— Fossil Butte has a history of cattle, horse, and sheep grazing. Before the establishment of the monument, the area was managed by the Bureau of Land Management. The area is still utilized by domestic livestock under grazing permits that will expire in 1983; grazing by cattle and sheep has influenced the native plant communities (Beetle and Marlow 1974). Heaviest grazing is in the wetter communities, Meadow and Willow-Aspen, and in the drier communities adjacent to these areas. Current management further concentrates animals by placing salt blocks in these areas. In addition, sheep are wintered on the monument. Quantitative data on livestock numbers and ranging patterns were not taken in this study. Beetle and Marlow (1974) noted that the combined grazing by both cattle and sheep during the spring rapidly inhibits annual vegetation production.

Discussion

Currently no data exist on the relative abundance of each species present in mammalian communities in the area with which to compare the results of this preliminary survey. The heavy, concentrated livestock use of the Meadow and Willow-Aspen communities and adjacent areas, which has resulted in an alteration of vegetation (close cropped vegetation, trampling, possible relatively high nitrogen content of soil, etc.), probably has in turn affected the distribution and abundance of at least some of the smaller mammals (e.g., *Microtus* complex). Since the area adjacent to the monument receives similar heavy livestock use, it would be difficult to find a control area to test this hypothesis. However, with the removal of livestock in the future, it may be expected that several mammals that are currently rare or non-existent on the monument but that are characteristic of the area will be found in greater numbers (e.g., *Sorex cinreus*, *S. vagrans*, *S. nanus*, and *S. palustris; Microtus pennsylvanicus*, *M. montanus*, *M. longicaudus*, and *Zapus princeps*).

ACKNOWLEDGMENTS

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AN UNDESCRIBED SPECIES OF *THELYPODIOPSIS* (BRASSICACEAE) FROM THE UINTA BASIN, UTAH

Stanley L. Welsh[1] and N. Duane Atwood[2]

Abstract.— *Thelypodiopsis argillacea* Welsh and Atwood sp. nov. is described from specimens collected on the Green River Shale Formation in Uintah County, Utah.

The impact of the Endangered Species Act of 1973 is being felt throughout the federal agencies that manage Utah lands. Intensified field investigations have yielded not only known taxa that are rare and potentially threatened or endangered, but also those that have not been previously named or described (i.e., those new to science). One of those new species is the one described below. The search that yielded the type material was undertaken to rediscover, if possible, living plants of the rare and obscure monotypic and endemic genus *Glaucocarpum.*

Although *Glaucocarpum* was not discovered until later in the summer of 1976, several other plants of interest were collected from the type locality of *Glaucocarpum.* Included among the collections were specimens of a crucifer, which is distinctive among the numerous Utah species. The presence of two narrowly endemic species, *Glaucocarpum suffrutescens* (Rollins) Rollins and *Thelypodiopsis argillacea* Welsh and Atwood, in the same general area is not altogether surprising when one considers the role that the common substrate (Green River Shale) has played as a spawning ground for narrow endemics. The obscure *Astragalus lutosus* Jones, for example, is also known from that formation, as are a number of other species.

In appearance and duration, *T. argillacea* is unlike any of the species of *Thelypodiopsis* in Utah. Those previously known from the state are all biennials, with well-developed basal leaves; the stems of *T. argillacea* arise from a branching subligneous caudex. The lowermost leaves are reduced in size; the others are merely sessile and not sagittate or auriculate as in the biennial species. In the diagnosis, *T. argillacea* is compared to *T. linearifolia*, a perennial species known from Colorado and Arizona to Mexico. *T. argillacea* differs from *T. linearifolia* in the salient features noted in the diagnosis inter alia.

The type material lacks mature siliques of the current season, and measurements of pods are taken from shattered fragments persisting on stems of the previous year.

Thelypodiopsis argillacea
Welsh and Atwood, sp. nov.

Thelypodiopsis linearifolia (Gray) Al-Shebaz aemulans, differt plantis parviores (13-30, nec 50-150 cm), foliis brevioris, petalis parvioris unguibus laminis nec distinguendis et siliquis et stylis brevioris et lobis stigmatis obtusis.

Plantae perennes omnino glabrae glaucae; caules 13–30 cm altus simplices vel ramificantes enascentes caudex sublignei; folia 9–35 mm longa 0.8-2 mm lata sessilia omnino caulina nec auriculata linearia leviter carnosa acuta vel rotundata; racemi (5) 8–22-floribus; pedicelli 7–18 mm longi adscendentes; sepala 4.2–6.5 mm longa violacea marginibus hyalinis; petala 7.8–10.9 mm longa 2.5–3.2 mm lata alba vel lilacina, venis purpuris conspicuis, ungue lamina nec

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distinguenda; antherae 1.7–2.5 mm longae; siliquae 18–25 mm longae 1–1.2 mm latae subsessiles teretes adscendentes vel erectae; styli 0.5–1 mm longi obconici; stigmata bilobata.

HOLOTYPE: Utah, Uintah County, hills west of Willow Creek, on the east slope of Big Pack Mountain, T10S, R20E, Sec. 33, at 5000 feet elevation, on Green River Shale, N. D. Atwood 6627, 11 May 1976 (BRY, isotypes to be distributed).

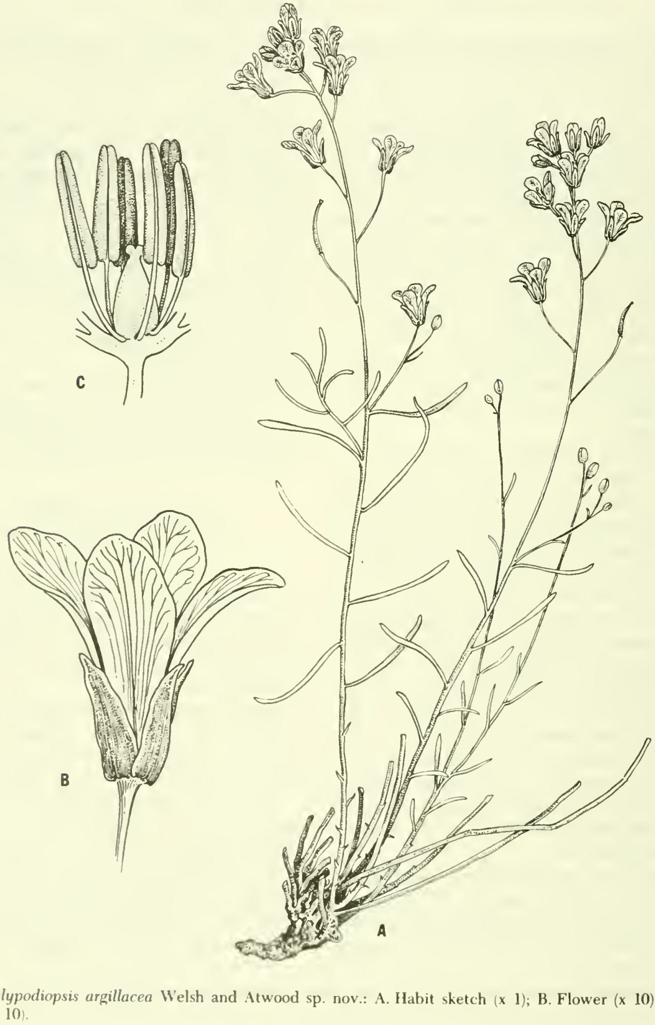

Fig. 1. *Thelypodiopsis argillacea* Welsh and Atwood sp. nov.: A. Habit sketch (x 1); B. Flower (x 10); C. Flower (dissected) (x 10).

A MOUNTAIN CERCOCARPUS POPULATION—REVISITED[1]

E. S. Nixon[2]

Abstract.— A mountain cercocarpus (*Cercocarpus montanus* Raf.) population was analyzed first in 1965 and again in 1975 to gain insight into the growth and reproduction of this species. The basis for comparison was plant height and number of basal stems. Growth (measured by height) was slow during the 10-year period, with plants on the northeast-facing slope having an average increase of 37 cm and those on the southwest-facing slope maintaining relatively the same average height. There was an overall decrease in average number of base stems for plants positioned on both slopes.

Located about six miles south of Chadron, Nebraska, near its eastern distributional boundary, is a rather small population of mountain cercocarpus (*Cercocarpus montanus* Raf.). During the summer of 1965, this entire population was analyzed by measuring the height and counting the number of basal stems on each shrub. This analysis was to provide a basis for future comparative studies. The objective of this study, therefore, was to reanalyze the population 10 years after the initial study to better understand the growth and reproduction of this shrub.

Although mountain cercocarpus provides shelter and browse for big game and is effective in erosion control (Richens 1967, U.S. Department of Agriculture 1974), little research in regard to its ecology had been done prior to 1960. Medin (1960) accomplished a rather detailed study of this species in relation to physical site factors and found that soil depth and moisture were the most significant factors affecting mountain cercocarpus production. Additional information is needed, however, to better understand the population dynamics of this species.

The mountain cercocarpus population in northwestern Nebraska was located on a hill that extended into a valley in a southeast to northwest direction. The vegetation of the valley was mainly mixed-grass prairie. The geographic position of the hill resulted in northeast- and southwest-facing slopes that ranged between 25 and 35 degrees. Mountain cercocarpus plants occupied both slopes.

The northeast-facing slope, which appeared to be more mesic, contained a fairly uniform canopy of ponderosa pine (*Pinus ponderosa* Dougl.) and a shrub layer consisting chiefly of wax currant (*Ribes cereum* Dougl.), prickly rose (*Rosa acicularis* Lindl.), western snowberry (*Symphoricarpus occidentalis* Hook.), poison ivy (*Rhus radicans* L.), common chokecherry (*Prunus virginiana* L.), and skunkbush (*Rhus trilobata* Nutt.). The dry southwest-facing slope exhibited a more open ponderosa pine canopy and a greater exposure of bare ground. The shrub layer consisted mostly of skunkbush and Great Plains yucca (*Yucca glauca* Nutt.). Grasses, sedges, and forbs were variously distributed on both slopes.

Methods and Procedures

Soils were analyzed at the Soil Testing Laboratory at Stephen F. Austin State University, Nacogdoches, Texas. Analyses included pH, Ca, P, K, Mg, soluble salts, and particle size. Surface samples were taken from the northeast- and southwest-facing slopes and from the ridge top.

Using the ridge top as the dividing line, mountain cercocarpus plants were divided into two groups, one associated with the

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northeast-facing slope and the other with the southwest-facing slope. Height and number of stems were recorded for each plant. Height measurements were taken from the soil surface to the tip of the tallest stem. Stem counts included those stems originating at the base of the plant.

Results

Soils

Soils of the study site, regardless of slope exposure, were generally similar. Texturally, they ranged from sandy-loam to loam. Nutrient concentrations, with the exception of P, appeared adequate for sustaining plant life (to 2275 ppm of Ca, to 31 ppm of P, to 300 ppm of K, and to 150 ppm of Mg). Soil pH ranged from 6.5 to 7.5, and soluble salt content was generally low.

Height Comparisons

Northeast-facing slope: Interestingly, the number of plants on the northeast-facing slope after 10 years was almost identical (425 plants in 1965 and 426 in 1975), resulting in a general shift in height of already existing plants (Fig. 1). In 1965 the greatest number of plants was in the 51–75 cm size class, whereas in 1975 the paramount size class was 176–200 cm. This is further substantiated by the occurrence of 98 fewer plants with heights between 1 and 150 cm as compared to 99 additional plants with heights between 150 and >300 cm. The average stem height in 1975 was 154 cm, a noticeable increase over the 1965 average of 117 cm.

Southwest-facing slope: Height growth trends were not as discernable on the southwest-facing slope (Fig. 1). There was a shifting of plants from the 51–75 cm size class to the 126–150 cm size class, indicating increased growth. A shift associated with the 201-225 cm size class peak in 1965 is barely observable, although, with the exception of the >300 cm size class, plants were generally taller. The average height of mountain cercocarpus plants in 1965 was 149 cm; in 1975 it was 144 cm.

The number of mountain cercocarpus plants on the southwest-facing slope increased from 360 to 397, an increase resulting from the establishment of a group of seedlings (Fig. 1). There were 36 more plants in the 1–150 cm category in 1975. The number in the 151->300 cm range, on the other hand, remained essentially the same (170 in 1965 and 171 in 1975).

Stem Comparisons

Northeast-facing slope: There was a reduction in the number of stems per plant during the 10-year period on this slope (an average of 10.9 in 1965 and 8.8 in 1975). Size class information indicated that in 1975 there were an additional 28 plants with 20 stems or less, and 27 fewer plants with more than 20 stems (Fig. 2). In 1965, 83 percent of the plants had less than 20 stems; in 1975, 89 percent had less than 20 stems. The reduction in number of stems for all mountain cercocarpus on this slope was from 4648 (1965) to 3755 (1975). Results were accentuated on the northeast-facing

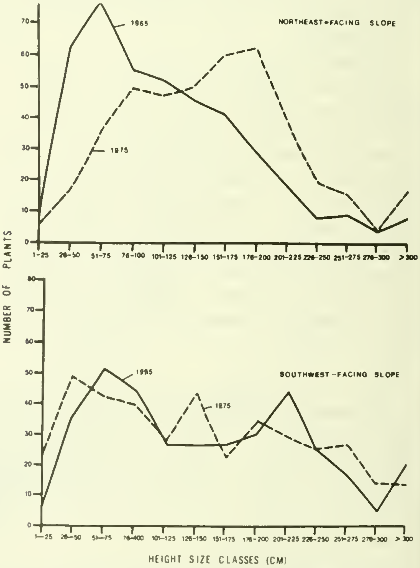

Fig. 1. Height comparisons of a mountain cercocarpus population sampled in 1965 and 1975.

slope because it appears that the same plants were present in 1965 and 1975.

Southwest-facing slope: The 10-year trend on this slope also indicated a general reduction in number of stems (11.5 stems per plant in 1965 as compared to 8.7 in 1975). Plants with 15 stems or more decreased in number by 32 plants. Those with less than 15 stems increased by 69 plants, but it should be remembered that much of this increase is attributed to reproduction. There were at least 37 new seedlings recorded in 1975. The overall reduction in number of stems on this slope was from 4139 to 3471.

DISCUSSION

Reproduction of mountain cercocarpus during the 10-year period from 1965 to 1975 was essentially non-existent on the northeast-facing slope, but had occurred in one particular location on the southwest-facing slope. If dependent on natural reproduction, seedling establishment appears to be very sporadic. This general lack of reproduction appears to be characteristic of this species, and seems to be due in part to seedling susceptibility to drought and frost (Plummer et al. 1968). Consequently, one- or two-year-old nursery-grown transplants with proper management are reported to have better chances of survival, and thus have been used in some instances to maintain or extend populations (Springfield 1972).

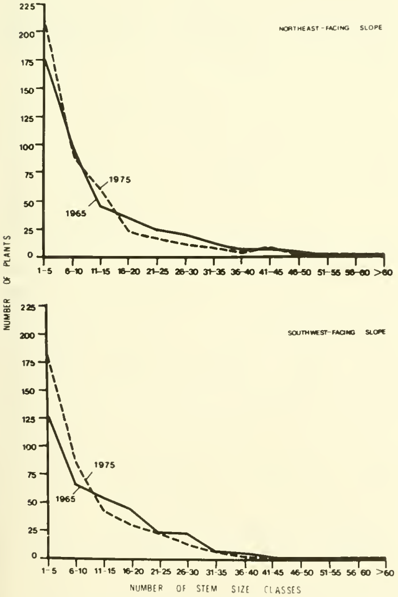

Fig. 2. Stem (number) comparisons of a mountain cercocarpus population sampled in 1965 and 1975.

Population dynamics over 10 years showed a general increase in height accompanied by a decrease in number of stems. Because of this reciprocal effect, it's doubtful that overall production was increased. The population appeared to be only lightly grazed by deer, so the consequence of grazing was minimal. Growth on the northeast-facing slope was more pronounced than that on the southwest-facing slope, due in part to seedling establishment on the southwest-facing slope and the fact that the seedling establishment lowered the average height. Medin (1960) found that soil depth, clay content of the A horizon, soil moisture, and surface stoniness (negatively) were site factors that contributed significantly to mountain cercocarpus production. This correlated very closely with results concerning the Nebraska population. The northeast-facing slope contained deeper soils, had a higher clay content in the A horizon, appeared more mesic, and was less stony than the southwest-facing slope.

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A NEW STATUS FOR *PENSTEMON CYANANTHUS* HOOK. SSP. *SUBGLABER* PENNELL (SCROPHULARIACEAE)

Stephen L. Clark[1]

ABSTRACT.— *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell, a plant found frequently in northwestern Utah, southeastern Idaho, and southeastern Wyoming, is elevated to species status. A new name, ***Penstemon holmgrenii*** Clark is proposed because *P. subglaber* is preoccupied.

Penstemon cyananthus Hook. ssp. *subglaber* Pennell is a tall, densely puberulent to pubescent, blue-flowered plant found commonly within sage and pinyon-juniper areas of northwestern Utah, southeastern Idaho, and southwestern Wyoming. Pennell described it in 1920 and separated it from *P. cyananthus* ssp. *cyananthus* on the basis that the leaves of the subspecies are more lanceolate and more densely puberulent. Investigations by this writer suggest, however, that other differences exist. *Penstemon cyananthus* ssp. *cyananthus* is never pubescent. The staminode of *P. cyananthus* ssp. *subglaber* is densely covered with long yellow hairs, and the two taxa are not sympatric. These differences suggest to the writer that the subspecies should be elevated to species status.

The following new name is proposed to replace the epithet *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell: *Penstemon holmgrenii* Clark nom. nov., based on *P. cyananthus* Hook. ssp. *subglaber* Pennell in Scrophulariaceae of the Rocky Mountain States. Contributions from the United States National Herbarium 20(9):313–381. Not *P. subglaber* Rydb. Named in honor of Arthur H. Holmgren, a friend who first guided me into studies in *Penstemon*.

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THE INFLUENCE OF PREDATOR CONTROL ON TWO ADJACENT WINTERING DEER HERDS[1]

Dennis D. Austin,[2] Philip J. Urness,[2] and Michael L. Wolfe[3]

ABSTRACT.— Two mule deer herds were studied on comparable, adjacent winter ranges in Utah. Significant differences in overwinter fawn survival were attributed to intensive predator control.

An unknown number of deer are continually killed on summer and winter ranges by predators, and in at least some locations these losses are significant. In Oregon, Trainer (1975), using radio-collared mule deer, found 14 percent fawn loss to predation in the first 45 days following birth, and 40 percent loss between January and April. Knowlton (1968) found that predation on fawns significantly limited deer population growth on the Welder Wildlife Refuge. Beasom (1974) showed a three-fold increase in the number of surviving fawns in a location of intensive predator control when compared to adjacent ranges in Texas. Smith (1976) compared fawn survival through January by comparing a herd enclosed by a predator-proof fence to an adjacent free-ranging herd; the enclosed herd had about twice the number of fawns/100 does. Conversely, other investigators (Ozoga 1966, Hancock 1974, Gipson 1974, Korschgen 1957) have indicated that predators have little influence on deer herds.

From 1973 to 1976 mule deer were studied on two adjacent pinyon-juniper winter ranges in northeastern Utah. Returns and observations from a deer tagging program indicated that both herds shared the Blue Mountain Plateau summer range. During late autumn one herd migrated into Miners Draw on the south side of the plateau, and the second herd migrated into the Cub Creek drainage on the west slope. Wintering herds were discrete, separated by about 11 km. Winter ranges were comparable in elevation, climate, and major browse species—big sagebrush (*Artemisia tridentata*), mountain mahogany (*Cercocarpus montanus*), and Utah juniper (*Juniperus osteosperma*). Browse utilization transects and field observations indicated that throughout the study deer numbers were well below carrying capacity on both ranges.

Predator control in the two areas greatly differed. Miners Draw, which received only limited control, was accessible by an unimproved road, and during the winter deep snow conditions often prevented any travel except via snowmobile. Consequently, this area received little use, and no predator hunters were observed in the area.

In comparison, the Cub Creek drainage was accessible via a paved two-lane road, becoming unimproved about halfway through the winter range. Both sections of this road were kept open by snowplows for two-wheel drive vehicles during most of the winter. A ranch was located in the lower portion of the area. Sheep, cattle, and horses were allowed to graze on the drainage throughout the winter. To minimize livestock losses, predators were intensively controlled by the owners and by a hired professional hunter-trapper. In addition, other predator hunters were occasionally contacted. The USFWS took approximately 80 coyotes in the Cub Creek drainage and 45 in Miners Draw during the winters from 1973 to 1976, and reported predator control work was less extensive in Miners Draw (personal communication, Bob Dickson, USFWS).

The number of visual predator observations, deer carcasses located, and deer densities between areas also differed. With approximately the same amount of effort expended in observation in both areas, only one coyote was observed in the Cub Creek drainage compared to nine in Miners Draw. Fifteen deer carcasses were found in Miners Draw; three of them were directly attributed to predation. Most of the others showed evidences of predation, but carcass conditions were too poor for accurate verification. In the Cub Creek drainage only two carcasses were found; one was evidently a road kill, the other was likely a poaching case. The mean deer densities for the two winters were six deer/km^2 in Miners Draw and 19 deer/km^2 in the Cub Creek drainage. The winter range in Miners Draw contained about 39.7 km^2; the Cub Creek drainage contained 29.8 km^2.

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[1] This study was partially supported by funds from the Pittman-Robertson Act under Project W105R.

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Deer classification counts were made during post-hunt and post-winter periods with 20x spotting scopes and binoculars. Data used included only those observations where all individuals within the group were positively classified (Table 1). Using an adjusted chi-square test, fawn and adult classification counts were not statistically significant between areas for the post-hunt periods 1973–74. However, counts were significantly different for the post-winter periods (1974 $X^2_{1.1.9} > .80$; 1975 $X^2_{1.1.9} > .80$; 1976 $X^2_{1.7.5} > .99$) as well as for all years combined ($X^2_{3.11.3} > .98$). Thus a significantly higher proportion of the fawns entering the winter period survived in the Cub Creek drainage, which had more intensive predator control, than did in Miners Draw.

TABLE 1. Fawn : adult ratios during post-hunt and post-winter periods (Fawns : 100 Adults)

	1973–74		1974–75		1975–76	
	Cub Creek	Miners Draw	Cub Creek	Miners Draw	Cub Creek	Miners Draw
Post-hunt	46	41	74	65	—	—
Post-winter	49	29	50	31	79	27

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PLANTS OF ARIZONA: A NEW SPECIES OF *ASTRAGALUS* FROM THE KAIBAB PLATEAU

Stanley L. Welsh and Kaye H. Thorne[1]

ABSTRACT.— *Astragalus atwoodii* Welsh and Thorne is named and described on the basis of materials collected on the Kaibab Plateau in Coconino County, Arizona.

In his discussion of *Astragalus pinonis* Jones, Barneby (1964, Atlas of North American *Astragalus*, Mem. N.Y. Bot. Gard. 13:259–261) discussed the existence of two collections tentatively ascribed to that species. Both collections are from Coconino County,Arizona. The first one cited (Goodding 92–49) is from South Canyon, south of House Rock Valley, and has not been examined by us. The other (Swapp 37) is filed in the collection of BRY. Dr. N. D. Atwood's recent collections in both flower and in fruit have been compared to the Swapp specimen. The specimens are a close match and demonstrate that the differences in ovule number as noted by Barneby (1964) hold constant for the Arizona materials. Further, the pods are consistently more slender than noted for *A. pinonis* sens. str. The terminal leaflet, always jointed to the rachis in *A. pinonis*, is occasionally confluent in the leaves of specimens from Arizona. Thus, the features of the Kaibab plants vary in approximately the same degree of magnitude as in other species of the section Lonchocarpi as defined by Barneby (1964).

It is proposed, therefore, that the plants from Arizona be designated as a new species, named to honor Dr. N. D. Atwood, tireless collector and student of the Hydrophyllaceae.

Astragalus atwoodii Welsh and Thorne, sp. nov.

Astragalo pinoni Jones aemulans, differt legumine angustiore (2.8–5.0, nec. 5.5–8.5 mm) et seminibus pauciore (18–22, nec 32–42).

Plantae perennes; caules erecti enascentes caudice subterraneis 1.9–5.7 dm altus, pilis basifixis adpressis; stipulae omnes distinctae; folia 0.6–9 cm longa; foliola (7) 9–17 (plerumque 13–17) linearia ad anguste oblonga obtusa ad rotundata 1.5–12.5 mm longa, 0.7–2.5 mm lata, foliolum terminale saepe confluens; pedunculi 4–7.5 cm longi; racemi 2–15-floribus 2–11 cm longi in fructum; bracteae tringulari-subulatae 1–2.2 mm longae; pedicelli 1–2.5 mm longi; calyces 5–6.5 mm longi strigulosi, tuba campanulato 3.5–4 mm longo, dentibus triangulari-subulatis 1.1–2.6 mm longis; flores ex purpureo ochroleuci 8–11 mm longi; legumina effusi-descendentes, subsessilia 21–34 mm longa 2.8–5 mm in diametros teretia vel dorsi-ventrali compressa strigosa rigide chartacei-coriacea brunnea grosse reticulata; ovula 18–22.

Holotype: Arizona, Coconino County, 17 miles southeast of Fredonia Sawmill, along logging road to Ryan, pinyon-juniper-cowania-big sagebrush community, N. D. Atwood 6794, 15 June 1976 (BRY, isotypes to be distributed). Additional specimens: Arizona, Coconino County; Kaibab Forest, T39 N, Rl E, Sec. 29, B. Swapp 37-S, 7 June 1926; do, 17 miles southeast of Fredonia Sawmill, N. D. Atwood 5053, 20 May 1973; do, 23 miles southeast of Fredonia Sawmill, N. D. Atwood 5055, 20 May 1973 (all BRY).

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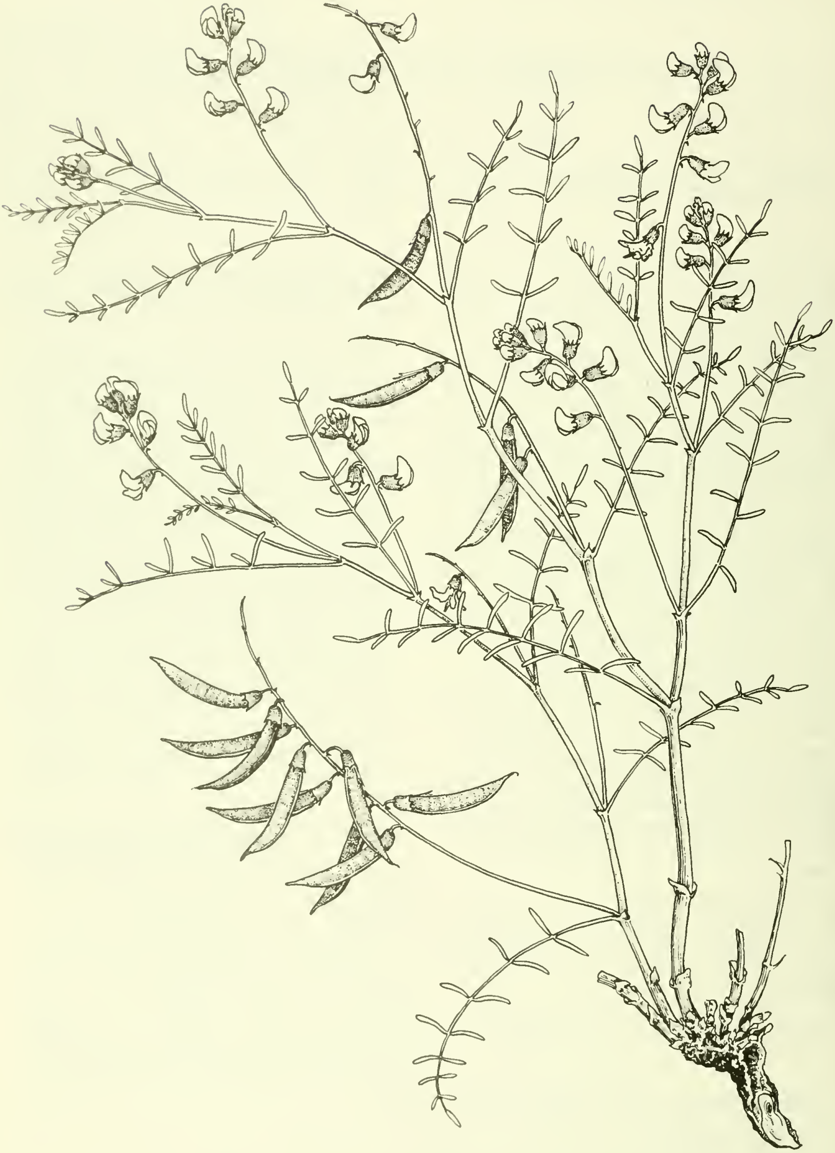

Fig. 1. *Astragalus atwoodii* Welsh and Thorne (x 1), drawn from Atwood 6794 and 5055 (BRY).

BIONOMICS OF TWO ASPEN BARK BEETLES, *TRYPOPHLOEUS POPULI* AND *PROCRYPHALUS MUCRONATUS* (COLEOPTERA: SCOLYTIDAE)

Jerold L. Petty[1]

Abstract.—Beetles of *Trypophloeus populi* attacked green bark of unhealthy aspen (*Populus tremuloides*) and hastened the death of the tree. Beetles of *Procryphalus mucronatus* favored dead bark and were of little significance in the death of the aspen. These two beetle species were distinguished from each other by their primary galleries, eggs, larvae, larval mines, and mating behavior. In *T. populi*, there were three larval instars and one to one and one-half generations per year; only larvae overwintered, and the eggs of the first generation were present by mid-July. In *P. mucronatus*, there were two larval instars and one and one-half to two generations per year; both larvae and adults overwintered, and the first eggs of the new season were present by late May.

In North America, quaking aspen (*Populus tremuloides* Michaux) occurs coast to coast from the 49th to the 69th parallel and sporadically at the higher elevations in the southwestern United States and in Mexico (Little 1971). These trees average from 12 to 15 m in height and from 30 to 60 cm in diameter (Preston 1969).

Aspen are important in several ways. Their role is well known as an intermediate (subclimax) cover species in plant succession, leading to the climax coniferous community (Oosting 1956, Krebill 1972). They recover quickly after extreme disturbances such as fire and clearcutting (Preston 1969). Directly, they provide browse for deer, elk, and livestock (Reynolds 1969, Wallmo 1972). Indirectly, they provide for a rich understory that in turn provides habitat for a diverse fauna and forage for livestock (Harper and Warner 1972). In the Rocky Mountains, the poplars (especially aspen) are the most important broadleaf trees and the only ones that could be considered usable as timber (Davidson and Hinds 1968). Aspen can produce more wood over a shorter period of time than conifers at comparable elevations (Davidson, Hinds, and Hawksworth 1959). Recently, they have become important as a timber resource (Lamb 1967). Aesthetically, anyone who appreciates nature cannot deny the unequaled beauty of a mountainside of aspen, especially in their cadmium hues of autumn.

The only American Scolytidae known to infest the bark of quaking aspen are *Procryphalus mucronatus* (LeConte), *Trypophloeus populi* Hopkins, and *T. thatcheri* Wood. Another scolytid, *Trypodendron retusum* (LeConte), attacks aspen, but it is a wood-boring ambrosia beetle. The published research on *P. mucronatus*, *T. populi*, and *T. thatcheri* has been mainly taxonomic. In fact, virtually nothing of a nontaxonomic nature has been written on the genera *Procryphalus* and *Trypophloeus*. Exceptions are a one-page article on the habits of the European *Trypophloeus binodulus* (Hagedorn 1904) and a half-page article on four European and Asian *Trypophloeus spp.* (Palm 1959).

There are only four known species of *Procryphalus* in the world, two in northern North America and two in northeastern Asia. In North America, *P. utahensis* Hopkins breeds in *Salix scouleriana* (Scouler Willow) and *P. mucronatus* in *Populus tremuloides*. There are 15 recorded localities for *P. mucronatus*, all of which are in the United States: Colorado 7, Idaho 2, New Mexico 2, and Utah 4 (Wood in press).

About a dozen species of *Trypophloeus* occur in Europe and Asia, but only four in North America. Of these four, *T. populi* and

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T. thatcheri are the only ones that have been collected from *P. tremuloides*. *Trypophloeus populi* also breeds in *P. acuminata* (Lanceleaf Cottonwood), *P. angustifolia* (Narrowleaf Cottonwood), and *P. trichocarpa* (Black Cottonwood). There are 13 recorded localities for *T. populi*: Arizona 1, Colorado 1, Nevada (eastern) 1, Utah 6, Idaho 1, Manitoba 1, New Brunswick 1, and Saskatchewan 1 (Wood in press).

The objectives of this paper were: (1) to report investigations on the life history and habits of *T. populi* and *P. mucronatus*, and (2) to determine the nature of the damage they cause in the host. Emphasis was placed on the differences between the two beetles in habits and behavior. It is hoped this research will establish a better understanding of the ecological significance of these species and provide a foundation for further studies of these and related scolytid species.

MATERIALS AND METHODS

Four sites were selected for this study, all of which were in Utah County, Utah. More than 80 percent of the total number of trees on each site were *Populus tremuloides*. The sites covered approximately 3,000 m^2 each and ranged from 2,256 to 2,377 m in elevation. The sites were initially selected by locating scolytid-infested aspen. The periods of study for each site and further details on the elevation, number of trees studied, and exact location of sites are given in Table 1.

Throughout the study, periodic collections and observations were made at the field research sites and in the laboratory at Brigham Young University from material brought from the sites. To facilitate observations, scolytid galleries were exposed by cutting away the bark with a razor-blade scalpel.

To rear the beetles, infested bolts, limbs, and bark sections were placed in 20-gallon, galvanized steel garbage cans, each of which had a pint glass bottle attached to collect the emerging scolytids. All rearing was conducted in the laboratory at room temperature. The number of larval instars was determined by measuring the width of the head capsules (Lekander 1968). Head capsules were measured from undamaged larvae and with an occular micrometer scale in a microscope at 80X magnification. The drawings of the larval head capsules (Figs. 22, 23) were composed from viewing 25 specimens of each beetle species under the light microscope and from 18 scanning electron micrographs of four specimens of each species. Photographs were taken with a Yaschica 35 mm SLR camera equipped with extension tubes and a flash. The margin of a millimeter ruler was included in many of the photographs for measurements. Details of the territorial behavior and mating ritual were obtained from extensive observations in the field and from movies obtained in the field with a Vivitar 8 mm movie camera equipped with a close-up lens.

A fungus was cultured from adult bark beetles by macerating them on the top of sterile pieces of aspen wood (four beetles per piece), and then placing each piece of wood upright on agar-agar medium inside petri dishes. The petri dishes were maintained at room temperature in the labora-

TABLE 1. Descriptions of research sites, Utah County, Utah.

Site No.	Locality	Elevation (m)	Pm[*]	Tp[*]	B[*]	DBH (cm)	Study period
I	1.6 km N Aspen Grove	2,256-2,259	8	2	2	30-50	VII-1972 to VI-1976
II	1.7 km N Aspen Grove	2,274-2,286	14	18	8	10-48	VII-1972 to VI-1976
III	2.4 km N Aspen Grove	2,365-2,377	0	12	2	31-49	VII-1975 to VI-1976
IV	1.9 km NE Squaw Peak	2,323-2,332	8	0	0	30-40	V-1973 to XI-1974

[*] These columns indicate the number of aspen trees studied at each research site that were infested with only *Procryphalus mucronatus* (Pm), with only *Trypophloeus populi* (Tp), and with both beetle species (B).

tory. When the fungus had grown out into the agar, the agar was removed intact and placed on the bark of a living aspen tree. To inoculate the tree, a razor-blade scalpel was inserted repeatedly into the bark by passing it through the agar. The agar was left on the tree. Three agar plates were used per tree. Subsequent observations were taken to determine whether or not the trees were dying. Three trees were inoculated in June and observed twice a month until October. The following year three observations were taken from June to October.

Results and Discussion

Trypophloeus populi

Behavioral sequence.—After locating the host tree, the female landed on the bark of the aspen and searched for a suitable site to begin the entrance of her primary gallery. When one female encountered another female who had already started her gallery, she paused and then continued her search, or tried to remove the other female and take over her entrance (see Territorial Behavior).

The site selected by the female to start the gallery was usually at a slight rough spot or irregularity on the surface of smooth living bark (Table 2). This apparently gave her better leverage to start the entrance. Sometimes this site was on or at the edge of a rough black spot (Fig. 4). The black spot made it difficult to see the beetle. This site was on the bole, limbs, or branches as small as 10 mm diameter.

Typically, the female directed the entrance into the bark at about a 30-degree angle from the surface (Figs. 14, 28) and upward from the horizontal (Table 2 and Fig. 3). In completed galleries, the entrance tunnel was about 2.5 mm in length and entered the primary egg chamber from the side (Table 2 and Fig. 1).

While the females were initiating their galleries, males (that had located the tree) began to search for them. When a male located a female that was initiating the gallery, he either stopped briefly and then went on to find another female, or he copulated with her (Figs. 14, 15) and then moved on.

The male behaved in a different way when the female was below the surface of the bark. After she backed up to the surface of the bark to remove boring dust, he mounted her (Fig. 28). Then, he tried to position himself and the female for copulation. He did this by vigorously stroking her with all of his legs. It appeared as though he was running in place. If successful, copulation followed, but usually this was repeated several times before copulation took place.

The female repeatedly backed part way out of and then returned into the gallery. Either this was part of her mating behavior

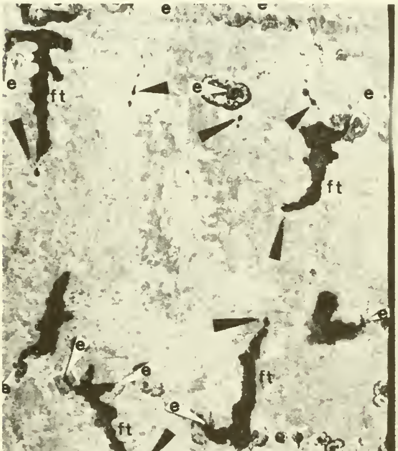


Fig. 1. *Trypophloeus populi*, primary galleries: 10 of the 13 galleries pictured were exposed by cutting away the epidermal bark covering them: e, white pointer marks the gallery entrance; black pointer, the parental adult exit hole; ft, the food tunnel; the circled arrow points upward.

TABLE 2. Details of 40 primary galleries from 4 trees (10 galleries each) 9 March 1976 (*Trypophloeus populi*).

Listing	Category	No. of Galleries
Bark surface at entrance		
	Slightly rough or irregular (Fig. 20)	31
	Black rough spot, entrance at edge (Fig. 4)	5
	Black rough spot	4
	Smooth	0
		Total 40
Blockage of entrance		
	Partially filled w/frass	18
	No blockage	18
	Plugged w/dead male	4
		Total 40
Angle of entrance above or below horizontal (degrees)		
	1–45 above	23
	46–90 above	9
	0–45 below	9
	46–90 below	0
		Total 41[a]
Bark covering gallery		
	Medium split (Fig. 6)	20
	Slight split (Fig. 1, unexposed galleries)	16
	Extreme split (Fig. 20)	4
		Total 40
Parents (dead) in the 14 galleries w/secondary chambers.[b]		
	Male and female[c]	7
	Female only[d]	4
	Male only	0
	Neither parent	3
		Total 14
Parents (dead) in the 26 galleries without secondary chambers.[e]		
	Unoccupied	17
	Male and female	5
	Male only	2
	Female only	2
		Total 26

[a] One gallery had two entrance holes.

[b] Exit holes were not present in any of the secondary chambers, and the epidermal bark covering them was not split

[c] In all seven galleries, the female was blocking the food tunnel entrance to the secondary chamber.

[d] In all four galleries, the female was blocking the food tunnel entrance to the secondary chamber

[e] There were 26 exit holes (18 in the food tunnel and 12 in the primary chamber)

or she was continuing her excavations. This interrupted the male's attempts to copulate with her. Because of the angle of the entrance into the bark, it was necessary for the female to back out of the entrance at least one-fourth of the way to be available for copulation.

After copulation, the male entered the gallery behind the female. If the gallery was not deep enough to accommodate both, the male entered as far as possible while the female continued to lengthen the tunnel.

As long as the male was protruding above the surface of the bark, another male could challenge him for his claim. This territorial competition was similar to that between females (see Territorial Behavior).

The female devoted her time to the excavation of the gallery, to oviposition, and probably to repeated copulation inside the gallery (observed on two occasions). She excavated the cavelike primary egg chamber at the inner end of the entrance tunnel. The design of this chamber was varied (Figs. 1, 2, 3) and sometimes consisted of two or even three distinct areas for the deposition of eggs. The female deposited a cluster of approximately 14 eggs in the primary egg chamber. They were deposited near to or against the paper-thin epidermal bark covering the gallery. Here, heat from the sun may have facilitated incubation, and aeration through the bark surface may have inhibited or prevented bacterial or fungal growth. Sometimes two or three clusters of eggs were laid in one gallery. Additional clusters contained fewer eggs (see Eggs). Very often a lone egg or two were deposited elsewhere in the gallery (Fig. 3). If eggs were located below subsequent excavations, frass accumulated on them (Fig. 2).

From the primary chamber, the female usually excavated a food tunnel (Figs. 1, 5, 6, f.t.) that was usually directed upward and extended approximately 10 mm. Frass collected in the tunnel behind her. Sometimes, she excavated a side pocket and deposited a few eggs therein. At the end of the food tunnel, she either died, exited by boring out of the tree, or excavated a secondary egg chamber (Figs. 5, 6, s.c.).

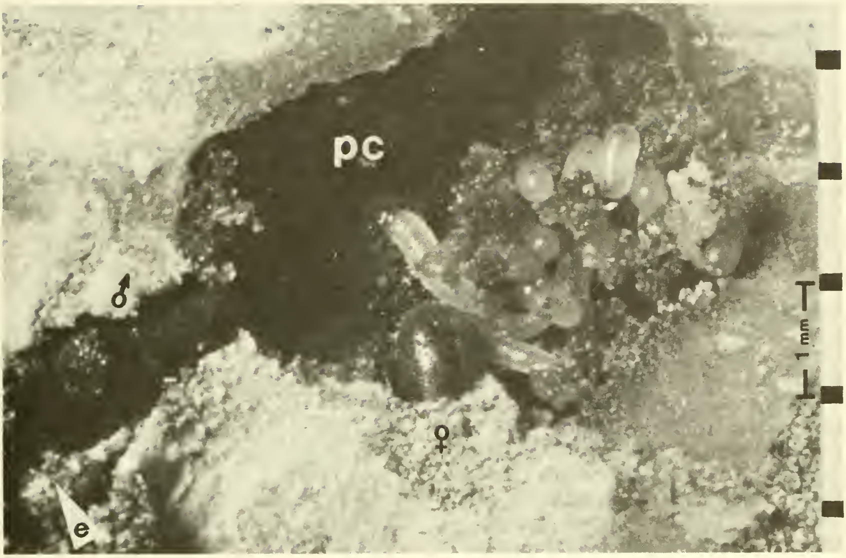


Fig. 2. *Trypophloeus populi*, partially exposed new primary gallery: pc, primary chamber.

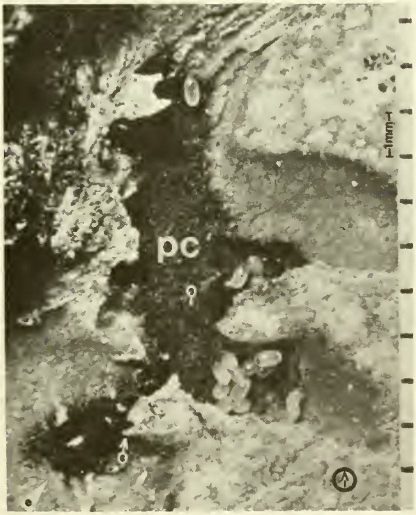


Fig. 3. *Trypophloeus populi*, exposed new primary gallery: pc, primary chamber; circled arrow points upward; parents (male blocking entrance), one and one-half egg clusters, and one lone egg.

During the period of excavation and oviposition, the male blocked the entrance to the gallery with his body (Figs. 2, 3). He died in this position, abandoned the gallery (by way of the entrance or by boring out through the bark covering the primary chamber), or followed behind the female as she excavated the food tunnel. Either one or both died or exited at or near the end of the food tunnel (Table 2). When the female excavated a secondary egg chamber, the male (if present) usually blocked the food tunnel at the point where it entered the secondary egg chamber (Fig. 5, s.e.) and helped remove boring dust by packing it behind himself in the food tunnel.

Once an egg hatched, the larva began its larval mine by boring into the wall of the primary gallery. As the mine in previously unexcavated bark was lengthened, it was also widened according to the growth of the larva. The dark brown to black frass deposited by the larva accumulated behind it and filled the mine. Here, it stuck together and dried, forming a firm blockage. The walls of the frass-filled mines were stained a dark brown color (Fig. 7). The larva excavated the first portion of its mine just under the bark epidermis (Figs. 6, 7). The length of this part of the gallery was approximately 20 mm, but this varied depending on the condition of the host, time of year, density of galleries, etc. This portion followed either a straight course, meandered, or reversed direction abruptly (Figs. 6, 7). At the end of this shallow excavation, the larva mined deeper into the bark (Fig. 6).

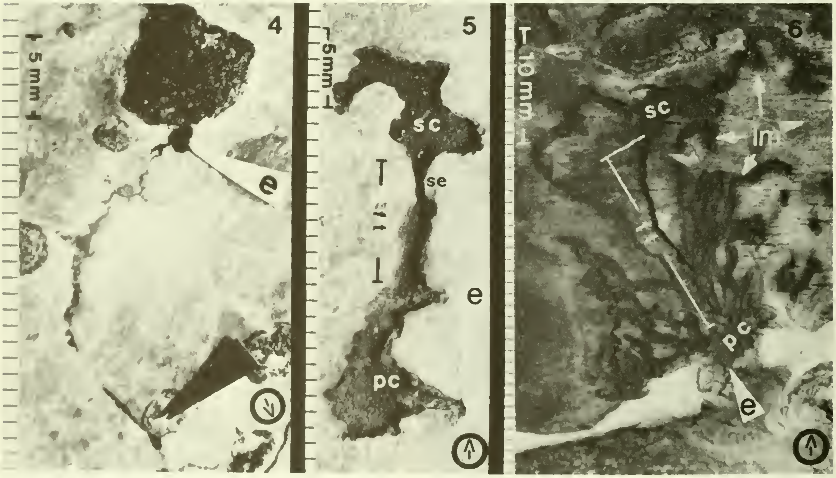
When the larva was mature, it excavated a frass-free pupal cell. In this cell it pupated and transformed into an adult. The new adult bored out of the bark and flew to find another tree to repeat the life cycle.

PRIMARY GALLERY.—Forty primary galleries, which had been excavated by bark beetles (*T. populi*) the previous season, were studied 9 March 1976 (Tables 2 and 3). Fourteen of the 40 had a secondary chamber. The bark lining the secondary chambers was darker in color (apparently stained) than in the primary chambers (Figs. 5, 6). In all 14, the bark covering the primary egg chamber and food tunnel leading to the secondary chamber was split, but this split did not extend into the secondary egg chamber.

Normally, each gallery was shared by one parental male and female. Occasionally one

TABLE 3. Measurements and details of 40 primary galleries from 4 trees (10 galleries each) 9 March 1976 (*Trypophloeus populi*).

Category	5 $\bar{m} \pm$ SD Range	n
Entire length	21 ± 7.2(10-14)mm	40
Maximum depth	2 ± .86(1-5)mm	40
Maximum width	4.6 ± 1.2(3-8)mm	40
Length of primary egg chamber	10.6 ± 2.8(7-20)mm	40
Length of food tunnel	10 ± 4.2(3-20)mm	20
Gallery orientation expressed in degrees to the vertical	72 ± 25.9(0-90)°	40
Percent of gallery filled with frass	60.5 ± 25.9(10-90)%	40
Percent of food tunnel filled with frass	67 ± 30.7(0.90)%	20



Figs. 4-6. *Trypophloeus populi*, details of three primary galleries entrance (e, white pointer), parental adult exit hole (black pointer), primary chamber (pc), secondary chamber (sc), secondary entrance (se), food tunnel (ft), the circled arrow points upward; 4, split bark covering primary gallery; 5, bark covering primary gallery removed; 6, bark covering primary gallery and larval mines removed.

gallery was connected to a neighboring one. Some galleries contained from one to three entrances. Excess parental adults appeared to be permanent residents of the gallery. The frequency of these exceptions was highly variable and increased with increased density of the beetles. Of the 10 exposed galleries in Fig. 7, one had two entrances, one contained a lone female, and one contained three females.

The angle of the entrance into the bark enabled the male to effectively block the entrance. In his blocking position the posterior surface of his elytra completely covered the entrance opening (Fig. 3, e.). If the entrance had been more nearly perpendicular to the bark surface, as in *P. mucronatus*, the ventral side of the posterior end of his abdomen would have been visible from the bark surface, and his elytra would not have completely covered the opening. This would have been to the advantage of predators, and rain could have entered the gallery more easily. The angle of the entrance into the bark, and the fact that it was usually directed upward from the horizontal, facilitated removal of frass and boring dust. In *P. mucronatus*, the entrance was often plugged with frass instead of the male.

The food tunnels studied were approximately 10 mm long. The reasons for the relatively great length of the food tunnel were not clearly understood. The fact that this tunnel was practically full of boring dust indicated that much more bark was excavated than was ingested by the female parent. Much of the boring dust found in the old primary galleries may have come from the excavation of the first part of this tunnel. The food tunnel may hasten the death of the bark in the surrounding area to the advantage of the larvae. The rate of mortality of the immatures was high in bark that remained alive. The greater the distance between a secondary egg chamber and the primary chamber, the less chance there will be of competition for space among the larvae of the gallery.

The fact that in some instances the female excavated a secondary egg chamber

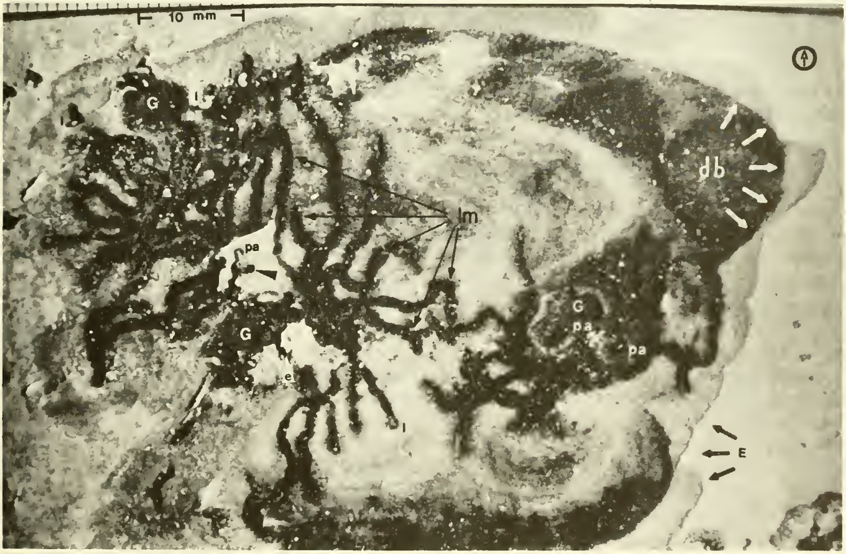


Fig. 7. *Trypophloeus populi*, exposed larval mines: lm, larval mines; l, larva; db, expansion of dying bark; pa, parental adult; E, edge of epidermal bark not cut away; G, primary gallery; white pointer (e), entrance to primary gallery; black pointer, parental adult exit hole; the circled arrow points upward.

and oviposited therein and in other instances she exited, indicated that if she did exit she was capable of excavating another primary gallery and ovipositing there also. Whether or not the female exits at the end of the food tunnel may be a function of the condition of the bark or the proximity of other galleries. If gallery density is high, it is expected that the incidence of secondary chambers would be low.

The male's habit of following the female while in the food tunnel suggests that he may copulate again with the female. His position at the food tunnel entrance may also prevent predators from entering.

EGGS.—The eggs were oblong, white, translucent, and had a tacky surface (Figs. 2, 3). Of 52 eggs measured, the mean width and length were .33 ± .030 x .65 ± .097 mm (Range .27-.42 x .55-.77 mm).

To estimate the number of eggs laid per gallery, the eggs and larvae in five primary galleries found 14 July 1973 were counted. The quantities per gallery were: 18 eggs and 3 larvae, 6 and 4, 11 and 6, 22 and 2, and 11 and 4. The parental adults were present and oviposition was probably not completed.

A primary gallery initiated 13 July 1974 and examined 3 August 1974 (21 days later) contained 15 eggs and 4 larvae (11 eggs and 3 larvae in one cluster, and 4 eggs and one larva in another). The gallery was 1.5-3.5 x 13 mm. Both parents were present and alive, the male blocking the entrance.

The tacky surface of the eggs normally held them together in a cluster in one area of the gallery. When frass fell on them, it adhered loosely. Apparently the parents did not remove this debris from the eggs because the eggs might be removed also.

Apparently the primary gallery protected the brood from predators and desiccation long enough for the eggs to hatch and for the larvae to mine out of it. After this, the bark covering the gallery usually split open (Fig. 4). The drying and shrinking of the gallery that followed appeared to make the entrances of the larval mines less accessible to entry by predators.

Predators may gain entry into the primary gallery when the male leaves the entrance to feed or copulate inside the gallery, and when the bark covering the gallery splits. The male may not need to leave the entrance to feed. Some of the borings pushed to him by the female might serve this purpose.

There are some problems created by laying the eggs in clusters. Egg mortality factors such as desiccation, predators, bacteria, and fungi would likely destroy whole clusters of eggs at a time compared to one egg at a time if they were oviposited as in *P. mucronatus*.

LARVAE.—The larvae were white, legless, and grublike (Figs. 2, 3). They appeared dark when their intestines were full of the brown bark. The relative length, distribution, and number of head capsule setae (Fig. 22) were characteristic of the species. The pattern of sclerotization on the frontal shield (Fig. 22, f.s.) may have been consistent in the last instar.

Widths of the head capsules of 232 larvae (Table 4) and numbers per size class (Fig. 24) indicate that there are three larval instars. Those .21-.28 mm, .30-.38 mm, and .40-.50 mm were categorized as Instar I, II, and III, respectively. These categorizations resulted in four size classes for Instar I, five for Instar II, and six for Instar III (Fig. 24).

In 24 scolytid species, Lekander (1968) found the average increase in larval head capsule widths from one instar to the next was 1.32 times (limits 1.20 and 1.48 times). By applying his method to *T. populi*, the average head capsule width increase (index) from Instar I to II and II to III was 1.31 and 1.35 times, respectively, compared to 1.33 from Instar I to II in *P. mucronatus*. The width of the head capsule in the last larval instar of *T. populi* was considerably wider (.46 ± .022 mm) than that of *P. mucronatus* (.36 ± .021 mm).

LARVAL MINES.—The larval mines were distinct and clearly separate from the primary gallery and usually from each other. The expansion of the dying bark surrounding the larval mines (Fig. 7, d.b.) indicated that the excavation accelerated the decline of the tree. The dark stain observed lining the mines may have been from oxidation of the bark or frass or both, or it may have been from fungi or bacteria associated with the beetle.

A dead tree in which emergence had taken place was examined 9 March 1976. The length of 16 larval mines (randomly selected) was from 26 to 42 mm (33 ± 4.5 mm). For additional information, larval depths and distances away from the primary gallery were measured from four trees containing live larvae 9 March 1976 (Table 5).

ADULTS.—Beetles were reared in the laboratory on various dates to determine the sex ratio and body lengths of the male and female (Table 6). The total reared (438 males and 587 females) gave a sex ratio of 1:1.34. A ratio of 1:1 was expected because of the importance of the parental male in blocking the gallery entrance.

From the 100 adults reared 7-13 April 1976 (Table 6), the first 50 to emerge (7-8 April) were longer (1.86 ± .106 mm, males, and 2.0 ± .097 mm, females) than the second 50 (1.8 ± .124 mm, males, and 1.9 ± .130 mm, females). The same was found in *P. mucronatus*.

In *T. populi*, the males were about 5 percent shorter than the females (widths were not determined). This was not expected because a male that is smaller than a female cannot block the gallery entrance as effectively as one the same size. These measurements were taken from emergent adults. The measurements of paired beetles in the primary gallery at the new tree may reveal less difference because of mortality of the smaller beetle during the flight to the new tree, and/or because of the replacement of the smaller beetle by a larger one in territorial behavior.

TABLE 4. Width of 232 larval head capsules (*Trypophloeus populi*).

n*	m ± SD Range (mm)	n**	Index Obtained
131	.26 ± .016(.21-.28)	7	.46/.26 = 1.71
50	.43 ± .016(.30-.38)	8	.46/.34 = 1.35
51	.46 ± .022(.40-.50)	6	.34/.26 = 1.31

*Sample size of larvae.

**Sample size of trees.

OVERWINTERING.—The larvae constituted the overwintering life stage (Tables 7, 8). Instars II and III survived at a higher rate than did Instar I. The contrast in the total number of each instar from one collection date to the next during winter was apparently due to the condition of the bark sampled and the differences in the dates when the trees were attacked.

The differences between the time material was brought into the laboratory for rearing and when the new adults began to emerge (Table 6) and the percentages of feeding larvae on different dates (Table 7), indicated that a dormant period occurred in the overwintering larvae and that it was controlled by something other than daylight and continuous warm temperature, because the rearing was conducted at room temperature and in the dark.

GENERATIONS PER YEAR.—The presence (Table 8), relative abundance of overwintering life stages (Table 7), approximate

TABLE 5. Depth of larvae in bark and proximity to primary gallery 9 March 1976 (*Trypophloeus populi*).

Instar	Distance from primary gallery m̄ ± SD Range (mm)	Depth from surface of bark m̄ ± SD Range (mm)	n*	No. of trees sampled and larvae/tree
II	7.5 ± 4.85(1-18)	.75 ± .75(.25-4)	40	2(20)
III	not determined	1.25 ± 1.01(.24-.4)	80	4(20)
III	6.6 ± 2.3(1-22)	not determined	60	3(?)
		Total	180	

*Sample size of larvae.

11-month duration of the life cycle in one tree in the field, and approximate 6-month difference between collection date (15 August 1972) and emergence date (February 1973) under laboratory conditions (Table 6), indicated that there were one to one and one-half generations per year in the field.

The overwintered Instar II larvae began to pupate and transform in late June. By early July they were emerging and attacking new trees, and by mid-July they were ovipositing in the new primary galleries (Table 8). This was a late start compared to *P. mucronatus* for the first eggs of the season.

TERRITORIAL BEHAVIOR.—The territorial behavior observed was basically similar to that described for *P. mucronatus*. However, the attempt of one beetle to dislodge the other by extension of the prothoracic legs (Fig. 26) was not observed.

The male that can do the best job of blocking the gallery is apparently selected for both strength and sufficient size to completely plug the entrance. A male that is smaller than the female that excavated the gallery entrance might be more easily displaced than one the same size.

LOCATING INFESTED TREES.—Infestations were found in stands of aspen where there

TABLE 6. Number and length of males and females reared on various dates, 1976 (*Trypophloeus populi*).

Collection date	Emergence dates	♂ (n)	♀ (n)	Lengths ♂ (mm) m̄ ± SD	Range	Lengths ♀ (mm) m̄ ± SD	Range
8 Mar[a]	7-8 Apr	18	32	1.9 ± .106	(1.7-2.1)	2.0 ± .097	(1.7-2.2)
	9-13 Apr	22	28	1.8 ± .124	(1.5-1.9)	1.9 ± .130	(1.6-2.1)
	14-18 Apr	10	13	Not determined		Not determined	
	Totals	50	73				
15 Aug[b]	Feb*	59	41	1.9 ± .153	(1.5-2.2)	2.0 ± .142	(1.7-2.3)
23 Apr & 24 May[c]	May & Jun	329	471	Not determined		Not determined	
	Grand total	438	587				

*Collected 15 August 1972 and emerged during February 1973.

[a]The most advanced life stage present was Instar III.

[b]The most advanced life stage present was Instar II.

[c]The most advanced life stage present was Instar II(?). Initial attack of this tree was estimated to be six weeks before collection date.

TABLE 7. Relative abundance of overwintering life stages of *Trypophloeus populi*.

Collection date	No. of trees sampled	Eggs	No. of immatures Instars I	II	III	Pupae	No. of adults Transformed*	Parental**	Feeding larvae (%)***
11 Nov 75	3	51	195[a]	39	8	0	0	5[c]	<10(?)
9 Mar 76	5	0[b]	34	194	122	0	0	0[d]	0
23 Apr 76	2	0	3	42	155	0	0	0	89
24 May 76	3	0	0	13	67	0	0	0	(?)
25 Jun 76	4	0	0	9	139	48	4	0	(?)

*In pupal cell or brood tree

**In primary gallery

***Percent of larvae that appeared dark because of bark in their intestines. All the rest were white—their gut devoid of food material.

[a]Of these larvae, 55 were dead. Of these 55, 35 were in the primary gallery.

[b]Though 6 eggs were collected, they were probably nonviable.

[c]Of 54 parental adults collected, 49 were dead.

[d]Of 60 parental adults collected, all were dead.

were many trees in the 30 to 50 cm DBH size. Unhealthy or diseased trees, especially those bordering washes, trails, roadways, and seepage areas, appeared to be particularly vulnerable to attack. In summer, the leaves of infested trees were usually stunted and lighter in color than normal. Susceptibility to attack seemed correlated with presence of the artist conk *Fomes applanatus* (Pers. ex Wallr.) Gill. Trees from which brood had already emerged typically had split bark above the primary galleries and exit holes where the transformed adults had emerged (Fig. 20).

HOST DAMAGE.—The beetles attacked living bark of unhealthy trees (Figs. 8, 9). At site II, 5 of the 18 (27.8 percent) infested trees studied harbored artist conks (*Fomes applanatus*). Typically, a single tree was attacked en masse, and the tree was covered with the galleries from the lower bole to the branches. Immature beetles died at a high rate in galleries that were in the smaller branches and in bark that remained alive after attack. The dying bark turned somewhat orange immediately around each gallery (Fig. 7, d.b.); the orange areas enlarged until they coalesced. The leaves died, the bark turned brown, and, within 3 to 10 weeks after the initial attack, the tree was virtually dead.

Three healthy trees were inoculated June 1973 with a fungus cultured from adult beetles. By July 1974 one of the trees had died; the other two remained healthy.

The decline of infested trees, expansion of dying bark tissue around individual galleries, and the death of one of the three trees inoculated with fungus cultured from adults indicate that this beetle has a definite

TABLE 8. Number of trees by calendar date containing the various life stages of *Trypophloeus populi* and *Procryphalus mucronatus*.

	Month									
Life stage	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec-Feb
T. populi										
Eggs	0[a]	0[a]	0	0	2	5	2	1	3	0[a]
Larval Instars										
I	4	1	0	0	4	1	2	1	3	0[e]
II	4	2	4	3	0	3	0[e]	0[e]	6	1
III	4	2	5	5	2	0	0[e]	1	2	0[e]
Pupae	0	0	0	5	1	1	0[e]	0	0	0
Adults in pupal cells	0	0	0	3	1	3	0[e]	0	0	0
Adults starting primary gallery	0	0	0	0	5	9	0[e]	0[e]	0	0
Adults in primary gallery	0	0	0	0	2	3	2	1	4	0
P. mucronatus										
Eggs	0[a]	0	2	7	7	4	0[e]	0	0	0
Larval Instars										
I	2	4	2	3	5	1	0[e]	0[e]	2	0[e]
II	2	4	3	0	4	5	0[e]	0[e]	4	1
Pupae	0	0	1	0	3	6	0[e]	0	0	0
Adults in pupal cells	2	2	1	2	8	6	0[e]	0[e]	4	1
Adults starting primary gallery	0	2	8	4	3	6	0[e]	o[e]	0	0
Adults in primary gallery	1	4	5	6	6	2	0[e]	0[e]	0[e]	0[e]

[a] A few eggs were found, but they were probably nonviable.

[e] This life stage was expected.

role in hastening the decline and death of unthrifty trees. A pathogenic fungus may be associated with the beetle.

The high mortality of immatures in the galleries that were located in bark that remained green after attack indicates that the rapid decline of the tree is essential for survival of the brood.

Unhealthy trees that might otherwise live on for several years evidently die within weeks if attacked en masse by the beetle. This appears to be beneficial to the survival of the aspen stand, since unhealthy trees harbor disease spores and rob understory and new aspen saplings of sunlight and moisture.

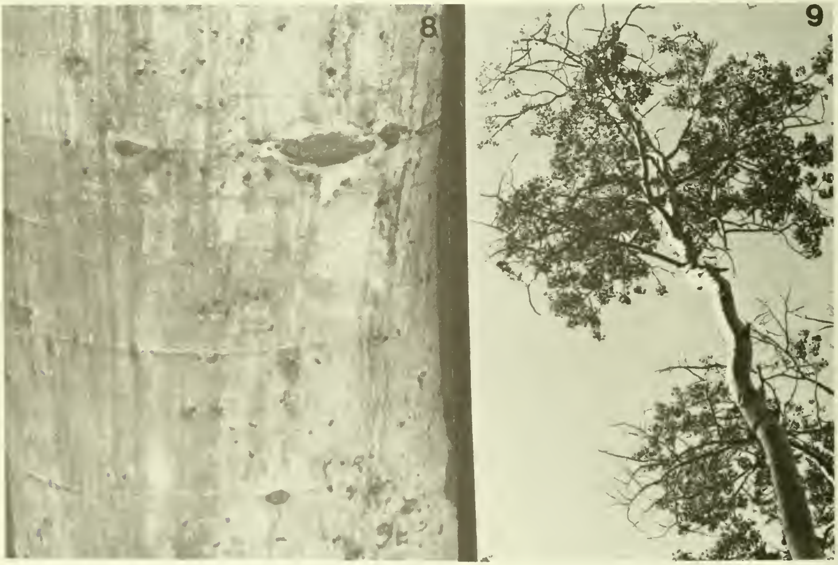
Procryphalus mucronatus

Behavioral sequence.—The behavioral sequence was basically the same as described for *T. populi*. The observed differences and other details are mentioned here and under subsequent sections.

Adults walking on the bark of the host held their antennae at right angles to the side of the head. In *T. populi* the antennae were extended forward at an angle of about 45 degrees from the side of the head.

After the male joined the female in the tunnel, the entrance was often blocked with a firm plug of frass. Some of the plugs observed in summer did not completely cover the entrance. Plugged galleries were found that contained only the female parent. Apparently, once the entrance was plugged behind an unpaired female, a male did not join her. Of 37 galleries studied 1 November 1975, the entrances of 35 were plugged completely. Of 90 studied 9 March 1976, all were unplugged. On a few occasions, a dead male was found in the entrance.

Both the male and female excavated the primary gallery. The female excavated the part of the tunnel where the eggs were deposited and the male apparently enlarged the gallery near the entrance (Figs. 16, 17). The female deposited each egg in a niche that she excavated and then packed it in with boring dust. The male apparently fed,

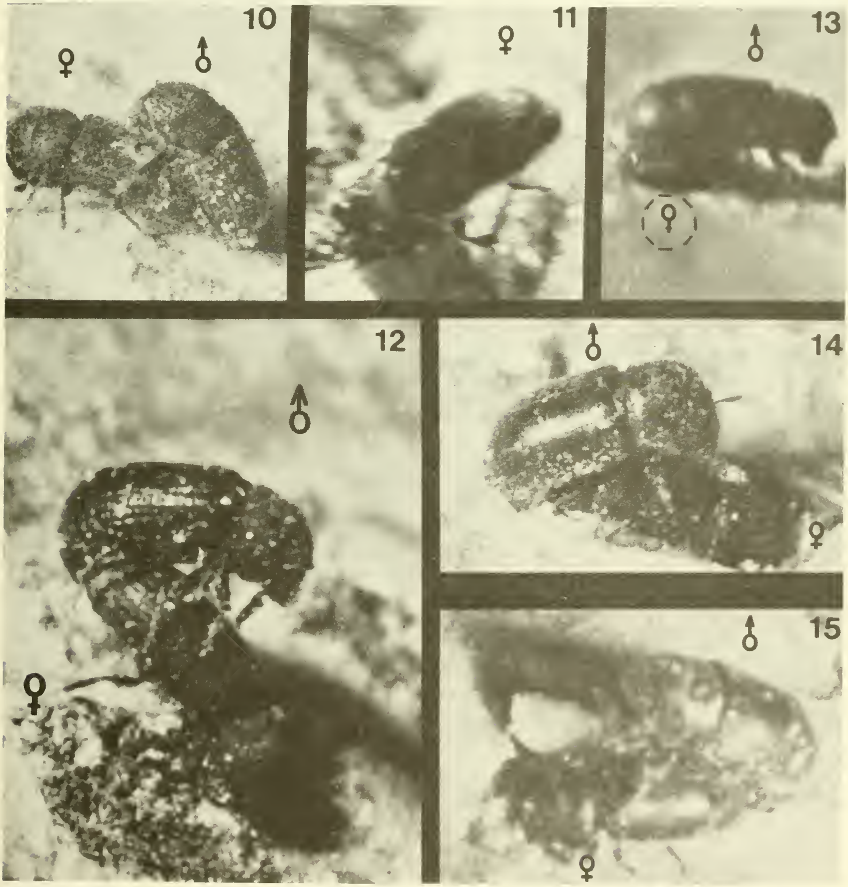


Figs. 8, 9. Aspen tree recently attacked by *Trypophloeus populi*: 8, distribution of gallery entrances (dark spots). 9, leaf condition (green and dying).

and remained available for repeated copulation.

After the eggs were laid, the parents died in the gallery. There was one exception to this. Parent exit holes were found in about 30 percent of the new galleries of two trees 25 June 1976. The trees were quite green. This may have been the reason that some of the parents abandoned the galleries.

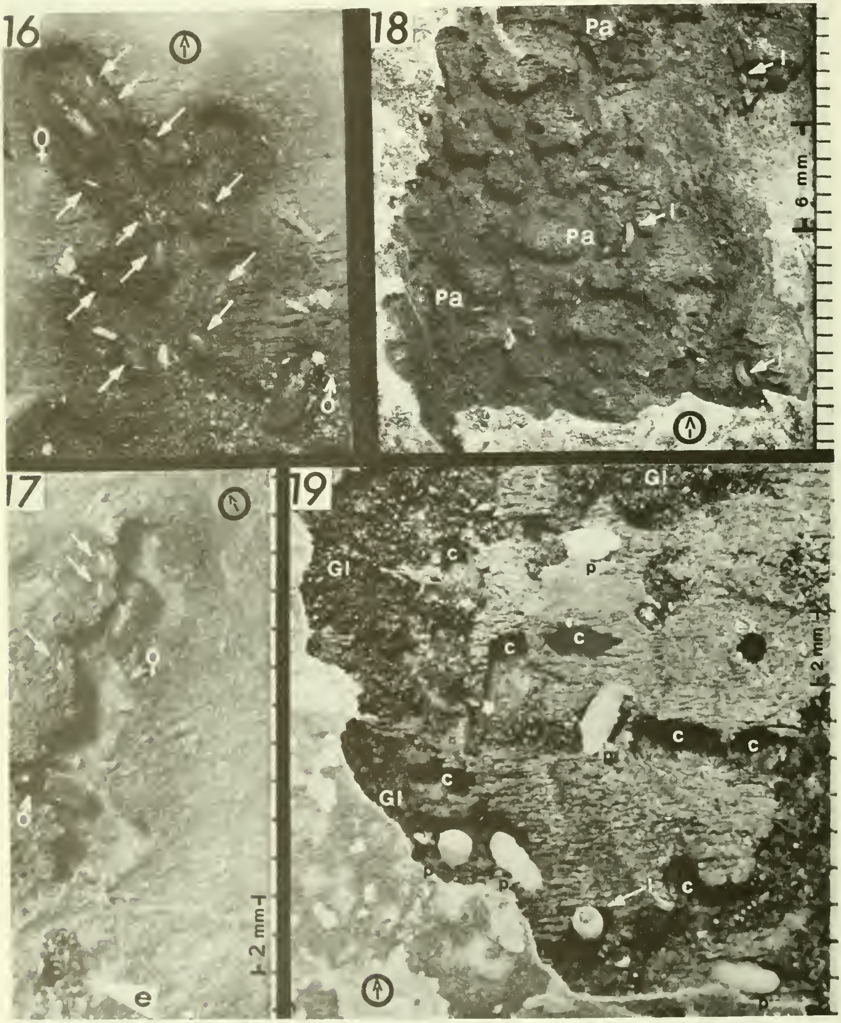
After the egg hatched, the larva began to feed, possibly first on the boring dust that surrounded the egg and then on the walls of the gallery. There appeared to be no relationship between the position of the egg and the direction in which the larva fed. Instar I and II larvae were commonly collected in the primary galleries that they had enlarged (Fig. 18). Instar II larvae and pupae were collected at the end of short larval tunnels (Fig. 19). Unlike *T. populi*,



Figs. 10-13. *Procryphalus mucronatus*, mating behavior: 10, male mating with female who is searching for a site to begin the primary gallery; 11, female starting the primary gallery; 12, male copulating with female who is starting the primary gallery; 13, male copulating with female who is in the gallery entrance. Figs. 14, 15. *Trypophloeus populi*, mating behavior: male copulating with female who is starting the primary gallery.

these tunnels were only partially filled with frass and the walls were not stained black.

After the larva was fully grown, it excavated and cleared a cell about .25 mm below the bark surface, where it pupated (Fig. 19) and transformed. After transformation, it fed, emerged, and attacked a new tree or reattacked the brood tree to repeat the life



Figs. 16, 17. *Procryphalus mucronatus*, exposed primary galleries: eggs (white arrows), and parents. Figs. 18, 19. *Procryphalus mucronatus*, larval excavations and pupae; pa, parental adult; l, larvae (Instar II); c, pupal cell; p, pupa; ex, exit hole of transformed adult; Gl, primary gallery that has been enlarged by larvae; circled arrow points upward.

cycle. If it was late in the season when the pupa transformed, it overwintered in the pupal cell.

PRIMARY GALLERY.—The primary gallery was: (1) approximately 14 mm long with tunnels from 1 to 3 mm wide that were straight or crooked and branched or unbranched (Figs. 16, 17), (2) usually directed upward (5 to 50 degrees from the horizontal) from the entrance, and (3) kept relatively free from frass. Ten galleries on 23 April 1976 were filled to approximately 35 percent with this debris. Other galleries examined in the summer (Figs. 16, 17) were free of frass. The question arises, how was frass removed when the gallery was plugged? It appeared that bacteria played an important role in reducing the size of the frass particles.

The following information was obtained from 25 galleries located July 1973: All contained eggs and parental adults, but no larvae. Galleries having their central axis approximately horizontal outnumbered two to one those that were approximately vertical (Fig. 17). Four entrances were located at the side, six at the top, and 15 at the bottom of the galleries. Nine of the galleries were fully branched (Fig. 16), 10 slightly branched (Fig. 17), 4 unbranched, and 2 had just been initiated.

Major differences in the primary gallery compared to *T. populi* were: (1) the main gallery was composed of comparatively narrow tunnels instead of broad chambers, and it was usually excavated in dead rather than live bark; (2) the bark of the bole or larger limbs, not the branches, was attacked; (3) the bark was usually soft and fermenting instead of firm; (4) the entrance tunnel was more nearly perpendicular to the bark surface, penetrated deeper into the bark (Fig. 27), and was often plugged with frass instead of being blocked by the male; and (5) the bark above the gallery did not usually split open (Fig. 21) as in *T. populi* (Fig. 20).

The excavation of the primary chamber and food tunnel in *T. populi* resulted in the splitting of the epidermal bark covering them, whereas the excavation of the secondary chamber in *T. populi* and the primary gallery in *P. mucronatus* did not cause the bark to split. The excavations that resulted in splitting were in dying bark that was green, whereas the excavations that did not result in splitting were in dead bark.

The angle at which the entrance tunnel penetrated the bark (Fig. 27) usually allowed copulation to take place when the male was on the bark surface (Fig. 13) without requiring that the female back out of the entrance. Compared to *T. populi*, the female was more protected in this position, and the male was closer to the bark surface; therefore, presumably both were less conspicuous to predators. The angle of the entrance into the bark may have also facilitated its being plugged because of the slight elbow created where the entrance tunnel curved to become parallel to the surface of the bark. The angle of the entrance, plugging of the entrance of the gallery, and gallery design need further study in relation to the condition of the bark and the time of year when the gallery is excavated.

EGGS.—The eggs were oval, white, translucent, and had a tacky surface (Fig. 16). Of 20 eggs measured, the widths and lengths were .38-.44 mm (.41 ± .016 mm) x .62-.76 mm (.68 ± .032 mm).

Eggs were counted from 20 primary galleries 25 June 1976. Because oviposition was apparently not completed in some of these galleries, only the 10 with the greatest number of eggs were used to compute the mean number of eggs laid per gallery. Galleries with more than one adult female were not counted. The mean was 16.8 eggs (Range 14-20).

Of 20 galleries studied during July 1973, the mean number of eggs per gallery was 8, with limits of 3 and 14; however, oviposition was not complete. Of 23 galleries studied that contained a total of 193 eggs, 95 were on the top, 60 on the bottom, 25 on the right side, and 13 on the left side of the primary gallery. This suggests an order of preference in egg placement.

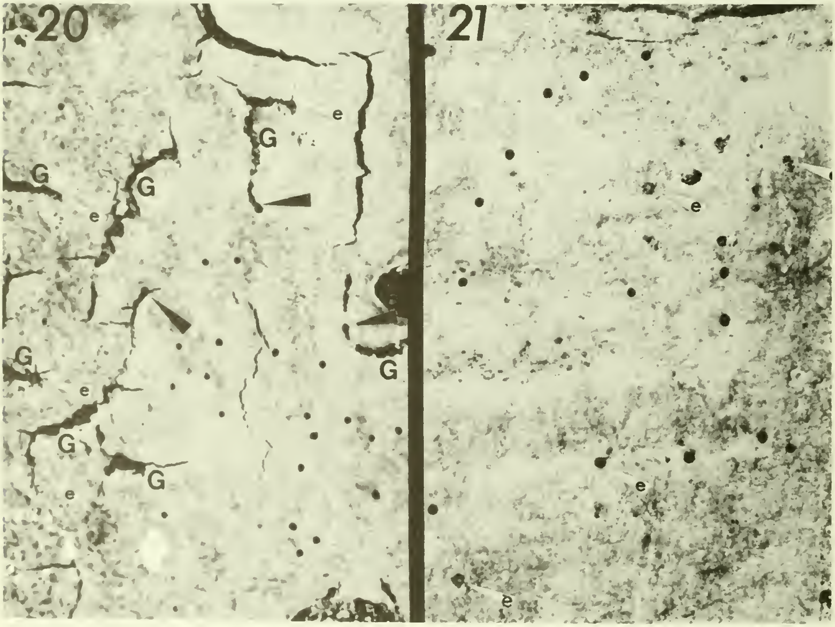
The eggs usually lined the tunnel walls (Fig. 16). They were deposited in rows or scattered throughout the margins of the tunnels of the gallery. The area of the gallery near the entrance where the male was located was usually free of eggs.

The incubation period for *P. mucronatus* was longer than for *T. populi*. The larvae were seldom collected with eggs, and one gallery contained 20 eggs with no larvae. Compared to *T. populi*, fewer eggs were laid and the female took greater care in depositing them, apparently to insure their survival. The larger size of the egg may be the reason why fewer were laid than in *T. populi*. The egg niche appeared to support, protect, and hold the egg in place. The boring dust packed around the egg (Figs. 16, 17) apparently holds it in place, insulates it, may serve for food when the egg hatches, and may protect it from predators.

LARVAE.—The superficial appearance of the larva was similar to *T. populi*. The length, distribution, and number of setae on the larval head capsule were characteristic of the species (Fig. 23). Widths of the head capsules of 91 larvae from 5 trees were measured as follows: 31 from 4 trees were .24-.29 mm (.27 ± .013 mm), and 60 from 5 trees were .33-.40 mm (.36 ± .021 mm). The index obtained from the means was: .36/.27 = 1.33. Those .24-.29 mm were categorized as Instar I and those .33-.40 mm as Instar II. Head capsules were wider than comparable stages of *T. populi*.

The feeding patterns of the larvae indicated that more bark per given area was utilized in *P. mucronatus* (Fig. 18) than in *T. populi* (Figs. 6, 7), possibly resulting in more larvae per unit area.

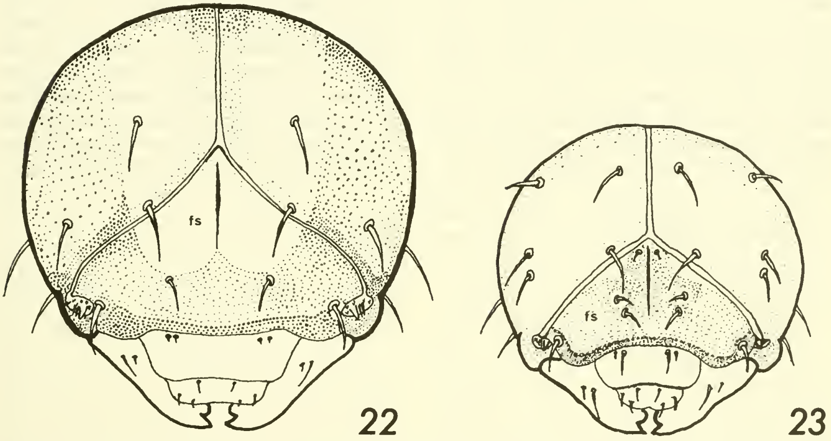
ADULTS.—The adults that emerged in the laboratory 5 February-1 March 1975 (163 and 237) and 30 March-5 April 1976 (75 and 170) all totaled gave the sex ratio (male:female) of 1:1.7 (Table 9). Lengths were determined for 100 of these emergents (35 males and 65 females). The males were 1.92-2.41 mm (2.20 ± .117 mm) and the fe-



Figs. 20, 21. Bark of dead aspen after brood has emerged; primary gallery (G), gallery entrance (e, white pointer), parental adult exit hole (black pointer), and exit holes of brood adults (unlabeled holes): 20, *Trypophloeus populi*, bark split above primary galleries; 21, *Procryphalus mucronatus*, bark not split above primary galleries and entrances plugged with frass.

males were 1.96-2.53 mm (2.29 ± .109 mm). These measurements were taken from emergents of 30 April, 2 May, and 3 May. The length means for the emergents of each of these days were 2.32, 2.29, and 2.26 mm for the females and 2.27, 2.18, and 2.21 mm for the males. The emergents of the first day were longer than the subsequent ones.

OVERWINTERING.—All life stages overwintered except the eggs and pupae (Tables 8, 10). There was mortality in the parental adults that overwintered in the new primary chambers, but some also survived. The empty gut appearance of larvae collected November 1975 and March and April 1976 (Table 10) indicated that the larvae were



Figs. 22, 23. Larval head capsules: fs, frontal shield: 22, *Trypophloeus populi* (Instar III); 23, *Procryphalus mucronatus* (Instar II).

Table 9. Number of reared males and females in the first hundred to emerge per week (5 February 1975 to 1 March 1975) and per day (30 April 1976 to 5 May 1976). (*Procryphalus mucronatus*).

Collection date	Emergence dates	(n)	(n)
29 Jan 1975	5-8 Feb	45	55
	8-19 Feb	27	73
	19-26 Feb	37	63
	26 Feb		
	1 Mar	54	46
	Totals	163	237
23 Apr 1976*	30 Apr	7	42
	1 May	13	36
	2 May	16	27
	3 May	17	23
	4 May	12	23
	5 May	10	19
	Totals	75	170

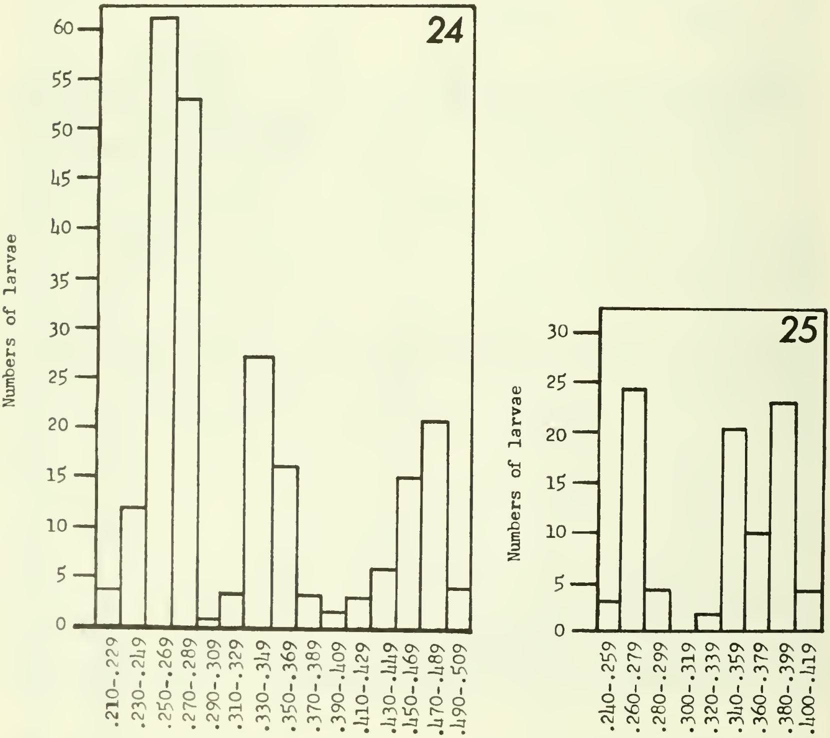
*Life stages present: adults and Instars I and II.

dormant during the winter. Overwintering larvae were found as deep as 7 mm from the surface of the bark. Because parental and newly transformed adults were found successfully overwintering, the adults may have some mechanism that enabled them to survive the cold winter months, a mechanism which was not present in *T. populi.*

The first eggs of the new season were laid fom one to two months earlier than in *T. populi.* The overwintered adults were ready to start new galleries and lay eggs as soon as the weather warmed up.

Seasonal occurrence.—The eggs of the first generation were found as early as 24 May. One tree was under initial attack 17 June 1972. By August 1972 (58 days later), pupae and newly transformed adults were present. In the laboratory rearing, the duration of time from the initial attack to the next generation was 60 days in one gallery.

The seasonal occurrence of the various life stages (Table 8), the abundance and presence of overwintering stages (Table 10), and the two-month life cycle in one tree in the field and in one bolt in the laboratory indicated that there were one and one-half to two generations per year and that the overwintered adults laid the first eggs of the next season. These were followed by the eggs laid by the adults that developed from the overwintered Instar II larvae. Adults that developed from the overwintered Instar I larvae may have a later egg-laying period.



Figs. 24, 25. Numbers of larvae per size class of head capsule widths: 24, *Trypophloeus populi*, 232 larvae measured from 8 trees; 25, *Procryphalus mucronatus*, 91 larvae measured from 5 trees.

TERRITORIAL BEHAVIOR.—The intraspecific territorial behavior consisted of the attempts of one beetle to take over another's place at the entrance to the primary gallery. Conflict for territory occurred between males and between females: between two females when one female tried to replace another female who had started her primary gallery, and between two males when one male tried to replace another male who had joined a female. The intruding beetle removed the resident by butting him (her) until he (she) backed out or was pushed out of his (her) entrance. This territorial behavior did not take place when the resident beetle was below the surface of the bark. At least half of the body of the resident needed to be protruding above the surface of the bark for an intruder to be successful.

Combat between females was observed as follows: (1) The intruding female butted the defending female until she backed out of her gallery. (2) Both beetles repeatedly met head on (prothorax to prothorax). In this position they butted each other back and forth (Fig. 26, a). (3) The beetle with the apparent advantage repeatedly extended her front legs (Fig. 26, b) in an effort to dislodge the other from the tree (Fig. 26, c). The asperities and marginal teeth on the prothorax appeared to be well adapted for butting and dislodging. Dislodgment of one of the beetles from the tree also resulted from butting without extension of the legs. Butting occurred head on, from the side, and from behind. Very often the less aggressive of the two contenders was driven away before dislodgment occurred. When an intruder located a defender who was too far into the gallery to be butted out, he either moved on or, apparently, tried to pull the defender out by clasping onto the posterior end of his elytra with his mandibles.

In both beetle species, the territorial behavior display was by the adult males, and females apparently selected for the more vigorous males at the new gallery.

MATING BEHAVIOR.—When a male located a female who was starting a gallery (Fig. 11), he either moved on or copulated with her (Fig. 12) and then continued to search for other females. For example, three males copulated in a 25-minute period with one female who was starting the primary gallery. The duration of each copulation was 5, 3, and 3 minutes. Copulations of one other female with three males lasted for 3, 8, and 10 minutes. Repeated copulations were commonly observed. On three occasions a male was observed copulating with a female that had not yet located a site to initiate the gallery (Fig. 10). This promiscuity apparently insured fertilization even though the females outnumbered the males nearly two to one. Lone females were frequently found in plugged galleries with eggs and larvae, but no parental male.

When a male located a female that was below the surface of the bark, he performed a mating behavioral sequence. The sequence

TABLE 10. Relative abundance of overwintering life stages of *Procryphalus mucronatus*.

			No. of immatures			No. of adults		
Collection date	No. of trees sampled	Eggs	Instars		Pupae	Transformed[a]	Parental[b]	Feeding larvae (%)[c]
			I	II				
11 Nov 75	3	0	27	63	0	86[d]	1[e]	<10(?)
9 Mar 76	1	0	4	76	0	20	0	0
23 Apr 76	1	0	20	24	0	0	0	84
23 Apr 76	4	0	P[f]	P[f]	0	0	P[f]	(?)

[a] In pupal cell or brood gallery

[b] In primary gallery.

[c] Percent of larvae that appeared dark because of bark in their intestines. All the rest were white—their gut devoid of food material.

[d] There were 60 females and 26 males.

[e] Female.

[f] Present, but numbers were not determined.

consisted of three distinct antics: nudging, stroking, and positioning.

Nudging: The male repeatedly nudged the female by brushing across the posterior end of her abdomen with his mandibles (Fig. 27). This motion was repeated from 6 to 12 times at a rate of approximately 4 per second (sample size: n = 18).

Stroking: The male vigorously (approximately 7 strokes per second, sample size: n = 1) stroked the female's abdomen with his prothoracic legs. It appeared as though he stroked both legs at the same time. He was positioned at the edge of the entrance (Fig. 27).

Positioning: The male put his mandibles

Table 11. Comparison of characteristics of *Trypophloeus populi* and *Procryphalus mucronatus*.

Category	*T. populi*	*P. mucronatus*
Attack	1. Live bark that is green—unhealthy trees 2. Mass attack—entire tree 3. Kills unhealthy trees	1. Dying bark that is orange or brown, fermenting, and soft 2. Scattered or mass attack—bole of the tree 3. Little effect on decline of host
Primary gallery	1. Cave-type plus food tunnel and secondary egg chamber 2. Parents often exit 3. Male blocks entrance 4. Bark covering gallery usually splits	1. Linear, tunnel-type 2. Parents seldom exit 3. Entrance often plugged with frass; male inside gallery 4. Bark seldom splits
Eggs	1. Egg cluster	1. Egg niches
Larvae	1. Three instars 2. Four prominent setae on frontal shield; 10 other prominent head capsule setae	1. Two instars 2. Six prominent setae on frontal shield; 14 other prominent head capsule setae
Larval mines	1. Distinct larval mines; fully plugged with frass	1. Larvae enlarge primary gallery; mines short, partially plugged with frass
Overwintering life stages	1. Larvae only	1. Larvae and adults
Generations per year	1. 1-1½	1. 1½-2
Territorial behavior	1. Butting	1. Butting and extension of prothoracic legs
Male mating behavior	1. Position directly over entrance 2. Nondescript stroking, all legs in motion	1. Position at edge of entrance 2. Nudging, stroking (prolegs only), positioning jerks
Antennal position when walking	1. Extended forward at 45-degree angle from side of head	1. Extended at right angle to side of head

in contact with the abdomen of the female. He apparently clasped the posterior margin of her elytra with his mandibles and also grasped her with his prothoracic legs. In this position, he often jerked the posterior end of his body up and down. He jerked from 5 to 11 times at a rate of approximately 2 per second (sample size: n = 11). It appeared as though he was trying to position her or stimulate her to position herself for copulation. She appeared to be very uncooperative. She repeatedly backed part way out of the entrance to remove boring dust and then went back in to continue excavation.

The sequence of nudging, stroking, and positioning took approximately 2, 3, and 10 seconds, respectively (sample sizes: n = 18, 18, and 8). The jerking antic (which was part of the positioning antic) took approximately two seconds (sample size: n = 11). The entire sequence was usually repeated several times before copulation was successful. From 3 to 30 minutes elapsed from the time the male located the female until copulation.

The apparent reasons for the mating antics were to insure intraspecific mating and prevent wasted time and energy in attempts to mate interspecifically. It was not unusual to find both *T. populi* and *P. mucronatus* attacking the same tree. The antics of *P. mucronatus* were more complex and apparently more advanced phylogenetically than in *T. populi*.

Locating infested trees.—Infestations of *P. mucronatus* were found in the same aspen groves as *T. populi* infestations and sometimes in the same tree. Diseased trees with fermenting bark were commonly attacked. Unhealthy trees typically died faster on the side that received the greater exposure to the sun. Sometimes *P. mucronatus* attacked this side while *T. populi* attacked the healthier, shaded side. Sometimes both species were in the same part of the tree, but *P. mucronatus* attacked several weeks after *T. populi*. Trees from which brood had emerged (*P. mucronatus*) did not have split bark covering the galleries, and many of the gallery entrances were still plugged with frass (Fig. 21).

Host damage.—Infested trees were usually diseased and infested with cerambycids and buprestids. The symptoms of the fungi *Cenangium singular* (Rehm.) Davidsen and

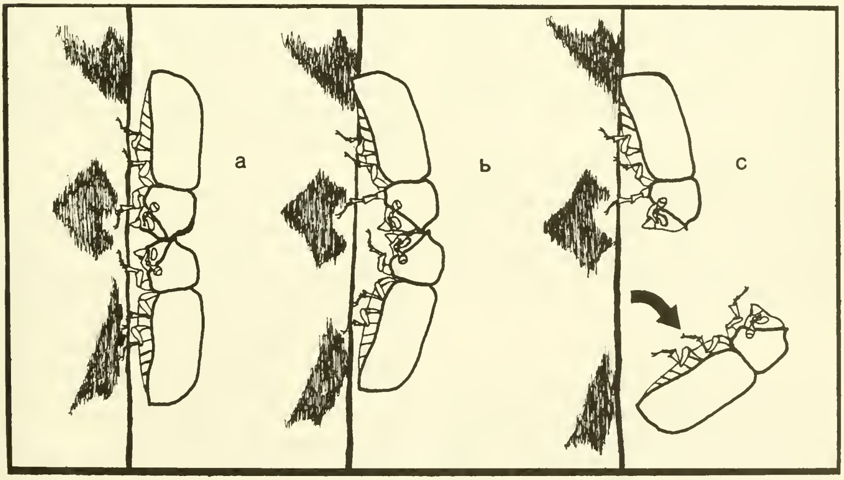
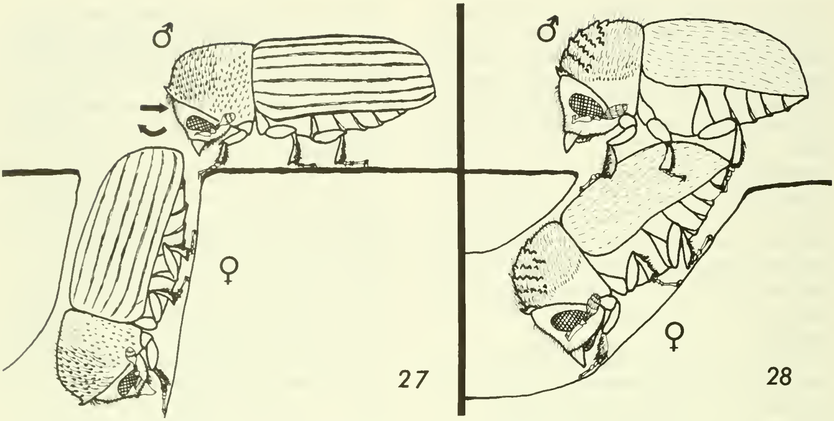


Fig. 26. *Procryphalus mucronatus*, territorial dislodgement behavior: a, butting; b, extension of prothorasic legs; c, dislodgement.



Figs. 27, 28. Mating ritual positions: 27, *Procryphalus mucronatus*; 28, *Trypophloeus populi*.

Cash, and *Cytospora spp.* appeared on many of the infested trees. The following beetles were reared from *P. mucronatus*-infested bolts: *Trypodendron retusum* (LeConte) (Scolytidae); *Saperda calcarata* Say, *Parallelina filicornis* Casey, and *Xylotrechus annosus* Say (Cerambicidae); and *Agrilus anxius* Gory and *Dicerca tenebrica* (Kirby) (Buprestidae).

Two trees were studied that were half dead. The bark of the dead half was heavily infested with *P. mucronatus*; nevertheless, the leaves that were present remained healthy and green from June to the end of the season.

These beetles (*P. mucronatus*) were seldom important in hastening the death of the host. They accelerated the decomposition process of dead parts of the tree. They tunneled and mined in the outer bark while the other borers attacked the cambium and xylem of the host.

Summary

There are behavioral aspects and morphological characters that clearly distinguish *T. populi* from *P. mucronatus* in all stages with the exception of the pupae, which were not studied in detail in this work (Table 11). Both species play an important role in the decomposition process of diseased and weakened aspen. Probably the most unusual discovery of this research was the territorial and mating behavior. An unexpected outcome was the success in locating *T. populi* in sufficient numbers to include it in the study. These beetles were associated with many other arthropods. Over 30 species of mites were collected from the beetles and their galleries. Most were phoretic; some were predacious. In addition, over 50 species of parasites and predators were collected and reared from the aspen infested with these beetles. A list of these species is in preparation.

Acknowledgments

This study was part of a Master of Science research project. The author thanks Dr. Stephen L. Wood for his direction and suggestions in the research and writing. Thanks are also extended to Dr. M. M. Furniss for his critical review, Dr. Samuel R. Rushforth for assistance with photography, Dr. Gary M. Booth for his suggestions, and to the late Dr. W. Dwight Buchanan for his help in rearing the bark beetles.

Special thanks are extended to my father, Dr. Wendell Petty, for his support and encouragement during this work.

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FOOD OF TOWNSEND GROUND SQUIRRELS ON THE ARID LAND ECOLOGY RESERVE (WASHINGTON)

Mark K. Johnson[1]

Abstract.— Diets of townsend ground squirrels were quantified from the Arid Land Ecology (ALE) Reserve in eastern Washington.

Little has been reported on townsend ground squirrel (*Spermophilus townsendi*) diets. Alcorn (J. Mamm. 21:160–170, 1940) stated that the species fed mainly on green vegetation. Davis (J. Mamm. 20:182–190, 1939) reported several species of plants in their diets. Scheffer (J. Mamm. 22:270–279, 1941) related the seasonal activity of the species to the seasonal abundance of green vegetation.

Twelve ground squirrels were live-trapped on the Arid Land Ecology (ALE) Reserve during March–May 1974 in an *Artemisia tridentata* (big sage)/*Agropyron spicatum* (bluebunch wheatgrass) association (Daubenmire, Wash. State Agric. Exp. Sta. Tech. Bull. 62:131, 1970). The ALE Reserve is 15 miles northwest of Richland, Washington, on the Energy Research and Development Administration's Hanford Works Reservation. This ground squirrel is not active above ground during the remaining months of the year at the elevation (1200 ft:366 m) of the study site.

The diet analysis technique employed was the same as that reported by Hansen and Flinders (Science Series No. 1, Range Science Dept., Colorado State Univ., 1969). Five microscope slides were made from the stomach contents of each ground squirrel, and 100 fields were quantified for each stomach sample.

There were 14 foods identified in the analysis: *Poa sandbergii* (49 percent), *Achillea lanulosa* (11 percent), *Lupinus laxiflorus* (10 percent), *Astragalus purshii* (11 percent), *Descurania pinnata* seed (8 percent), *Erigeron filifolius* (3 percent), *Antennaria dimorpha* (2 percent), *Salsola kali* (2 percent), *Artemisia tridentata* (2 percent), *Sisymbrium altissimum* (2 percent), unclassified forb (3 percent), *Balsamorhiza careyana* (<1 percent), *Lactuca serriola* (<1 percent), lichen (<1 percent) and arthropod (○1 percent).

Staple foods of townsend ground squirrels were almost entirely green vegetation. The above-ground activity of the species seemed to be highly correlated with the seasonal abundance of the major food, *Poa sandbergii*.

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HOST-INDUCED MORPHOLOGICAL VARIATIONS IN THE STRIGEOID TREMATODE *POSTHODIPLOSTOMUM MINIMUM* (TREMATODA: DIPLOSTOMATIDAE). II. BODY MEASUREMENTS AND TEGUMENT MODIFICATIONS

James R. Palmieri[1]

Abstract.— Extensive feeding experiments were undertaken to determine if physiological host specificity was a major characteristic of *Posthodiplostomum minimum.* This involved the feeding of experimentally infected sunfish livers containing metacercariae of *P. minimum* to amphibian, reptilian, avian and mammalian hosts. Host-induced morphological variations of adult *P. minimum* were shown to be associated with the genus and class of host employed as well as with the inherent variability of *P. minimum* exclusive of host factors. Morphological characters such as body size and shape and tegumental surface and spines are indicated as undergoing morphological variation. Of all the experimental definitive hosts used, avian and mammalian are the most suitable for normal development of *P. minimum.* Amphibian and reptilian hosts demonstrate marked variation in the adult worm development usually manifested by pronounced size decrease.

Posthodiplostomum minimum (MacCallum, 1921) is a strigeoid trematode of the family Diplostomatidae Poirier, 1886. Adults of this species (Fig. 30) parasitize the intestine of piscivorous birds and the metacercarial stage is found in various freshwater fishes.

Two subspecies of *P. minimum* have been reported, based upon the ability of cercariae to penetrate and develop either in centrarchid or cyprinid fish hosts (Hoffman, 1958). The subspecies used in this investigation is the centrarchid strain (Palmieri 1975).

Since Stunkard's report on intraspecific variation in 1957, several more recent experimental studies have shown that size, shape, and position of various organs and structures in helminths may be considerably modified by the host. For many years, investigators such as Dubois (1944, 1955, 1968, and 1970) have delineated species of strigeoids largely on the basis of host specificity. Recently, however, several investigators have shown that parasites can indeed develop within hosts that normally would be ecologically isolated from involvement in the normal life cycle of the parasite (Blankespoor 1971, Campbell 1972, Palmieri 1973, Ulmer 1961, Watertor 1967).

The lakes region of northwestern Iowa is an area rich in conditions requisite for the production of both snail and fish intermediate hosts of *Posthodiplostomum minimum.* This area also serves as both a feeding and nesting area for piscivorous avian hosts needed in maintaining the life cycle of *P. minimum.*

Experimental infections of a variety of amphibian, reptilian, avian, and mammalian hosts with experimentally developed metacercariae of *P. minimum* were carried out from 1971 to 1974 at Iowa State University and the Iowa Lakeside Laboratory. Adult *P. minimum* recovered from these ecologically abnormal hosts were examined for host-induced morphological variation.

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MATERIALS AND METHODS

Three eggs of *Posthodiplostomum minimum*, obtained from a single gravid worm from an experimentally infected chicken 48 hours postexposure, were placed in an embryological watch glass with filtered lake water. Hatching of the miracidia occurred 20 to 21 days later.

A single miracidium was exposed to a laboratory-reared *Physa gyrina* and pentration was observed. This snail was isolated in a one-gallon aquarium and maintained in the laboratory until shedding of cercariae took place (48 days postpenetration). Twice daily for 10 days, contents (shed cercariae) of the one-gallon aquarium were poured into an aquarium containing parasite-free, laboratory-maintained sunfish. Once infected, sunfish were then maintained at room temperature for 45 days. These sunfish livers served as the source of metacercariae for subsequent experimental feedings to definitive hosts.

All definitive hosts which had been exposed to laboratory-developed metacercariae were autopsied from 49 to 96 hours postinfection. Adult worms so obtained were washed in the appropriate Ringer's solution and were prepared for light microscopy or scanning electron microscopy.

Microscopy.—Specimens to be examined by scanning electron microscopy were fixed in a modified Parducz (1967) fixative (6.0 ml of 2 percent O_sO_4 and 1.0 ml of saturated mercuric chloride) for one minute at 0 C. All specimens were then washed in distilled water three times at 15-minute intervals. Entire specimens were rapidly dehydrated in ethanol using critical point drying techniques as described by Hearle, Sparrow, and Cross (1972), Cohen and Shaykh (1973), Polliack, Lampen, and de Harven (1973), and Lewis and Nemanic (1973).

Dried specimens were then affixed by electrically conductive aluminum paint to cleaned brass plates and secondarily affixed to brass specimen holders. Specimens were initially coated with carbon and were subsequently given a double coat of gold-palladium. All specimen coating was done with the aid of an Edwards vacuum evaporator. Coated specimens were viewed and photographed on a Jeolco JSM-Sl scanning electron microscope at an accelerating voltage of 10 KV. All micrographs were recorded on Kodak Ektapan 4162 negative film and developed in a mixture of six parts Kodak D-76 and one part Kodak D-19 for maximum resolution and negative contrast.

Experimental Infections.—Definitive hosts were force-fed sunfish livers experimentally infected with over 100 metacercariae of *P. minimum*. Once fed, all hosts were maintained in appropriate cages or aquaria and fed only water. After a suitable developmental period of 49 to 96 hours, these hosts (Table 1) were examined for the presence of *P. minimum* adults, using standard routine laboratory methods. Details of all hosts exposed to cercariae and those fed metacercariae of *P. minimum* have been reported by Palmieri (1976).

RESULTS AND DISCUSSION

Body Measurements.—Five variables and relationships were analyzed for the body measurements of *P. minimum* (Table 1). These include (1) body length (BL) (from the anterior margin of the forebody to the posterior of the hindbody, exclusive of the extended bursa, when present); (2) body width (BW) (at the widest portion of the forebody); (3) distance from the anterior

TABLE 1. Total number of vertebrate hosts exposed to fish livers experimentally infected with metacercariae of *P. minimum*.

Class	Positive	Negative	No. Species	Total No. Hosts
Amphibians	17	4	4	21
Reptiles	8	2	3	10
Birds	18	9	8	27
Mammals	13	9	6	22
TOTAL	56	24	21	80

margin of the forebody to the anterior margin of the acetabulum (DAA); (4) from the posterior margin of the acetabulum to the posterior margin of the hindbody (DPP); and (5) the ratio of DAA/DPP. This relationship (DAA/DPP) was chosen rather than forebody and hindbody lengths because of the lack of uniformity of a distinct demarcation between these regions in some specimens. It was also decided that using the ratio DAA/DPP would minimize the effect of size differences of adults of *P. minimum* because the position of the acetabulum is relatively constant and serves as a more uniform reference point. A complete tabulation of the above data follows in Table 2.

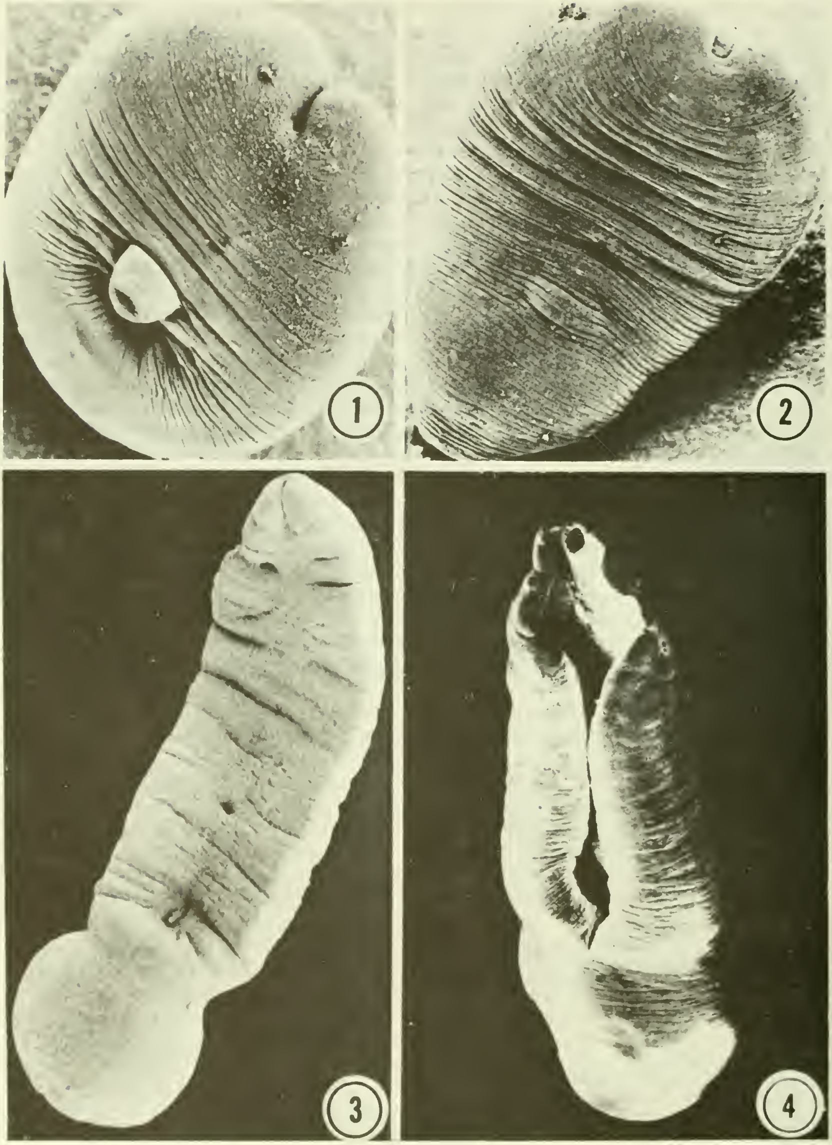
Body size (length and width) of adult *P. minimum* is a significant characteristic in identifying the class of definitive host used for experimental development of adult worms. At the class level, both body size and position of demarcation between the forebody and hindbody regions of *P. minimum* vary significantly. In worms recovered from amphibian and reptilian hosts, very little demarcation can be noted (Figs. 1–3, 9–13). Furthermore, in many worms developed within these poikilothermic hosts, considerable invaginations of the anterior margin of the forebody occur (Figs. 11–12). In many worms the hindbody is not present (Fig. 1–2) or is poorly developed (Fig. 3). In some experimental avian hosts fed metacercariae of *P. minimum*, however, adult worms appear normal and well developed with a well-demarcated forebody and an elongate, cylindrical hindbody (Figs. 6, 8, 14, 16–19). In the most common definitive host for *P. minimum*, the great blue heron, worms recovered from this naturally infected host demonstrate the most characteristic body form (Fig. 19). Those worms recovered from mammalian hosts appear to be more normal in their development than those recovered from amphibian and reptilian hosts but vary somewhat from those recovered from avian hosts in possessing hindbodies whose lengths are reduced in proportion to the forebody (Figs. 4, 5, 7, 15, 17, 18, 20–21).

Tegumental modifications.—Several host-induced modifications of the tegument were noted during the course of this study. Scanning electron microscopy of the tegument of *P. minimum* specimens recovered from a variety of experimentally fed hosts revealed that tegumental spines underwent morphological modification. Two regions of the adult worm were selected for observa-

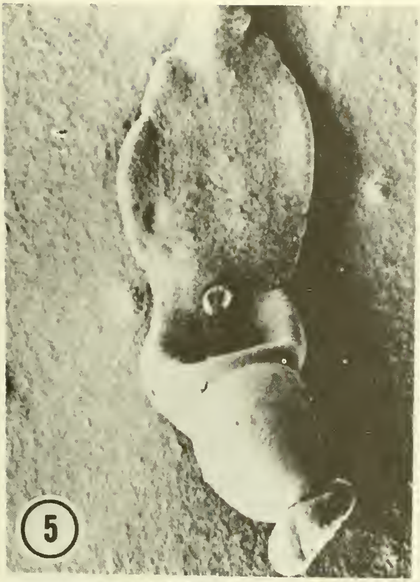
TABLE 2. Body measurements of *P. minimum* from experimental definitive hosts.[1]

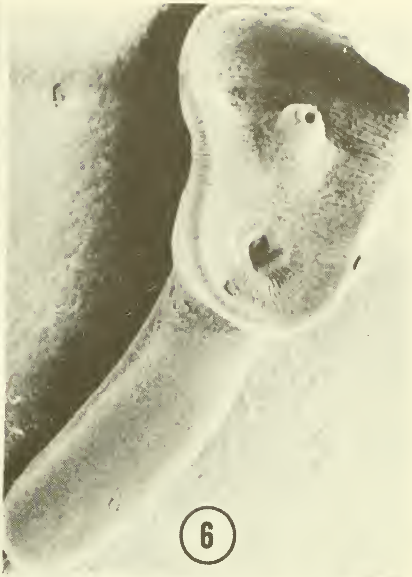
Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Body Length (BL)	0.534	0.083	0.517	0.435	0.614	0.589
Body Width (BW)	0.273	0.043	0.269	0.230	0.288	0.296
Distance from Anterior Margin of Body to Anterior Margin of Acetabulum (DAA)	0.188	0.056	0.203	0.120	0.210	0.184
Distance from Posterior Margin of Acetabulum to Posterior Margin of Body (DPP)	0.260	0.067	0.243	0.198	0.321	0.274
Ratio of DAA/DPP	0.735	0.238	0.867	0.554	0.664	0.634

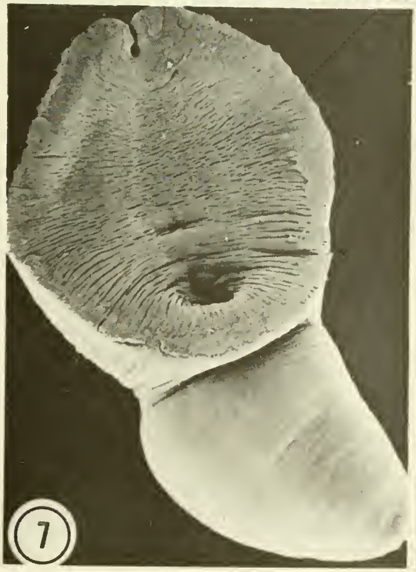
[1] All measurements in mm

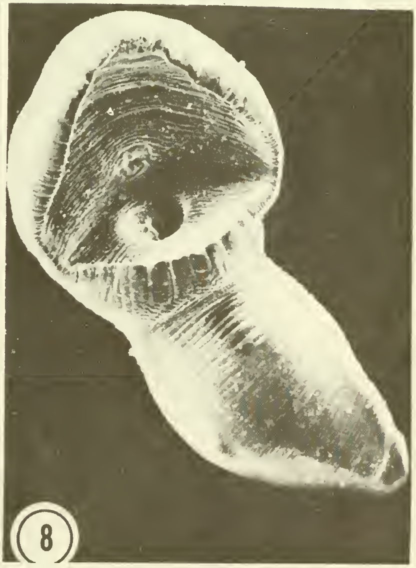


Figs. 1–8. Morphological variation of body shape of adult *P. minimum* recovered from vertebrate hosts. Note variations in body shape and hindbody demarcation. All specimens 72 hours old (Scale: 1 inch = .120 mm). Hosts are: 1, *Bufo americanus* Note lack of hindbody; 2, *Amblystoma tigrinum* Note lack of hindbody; 3, *Chry-*

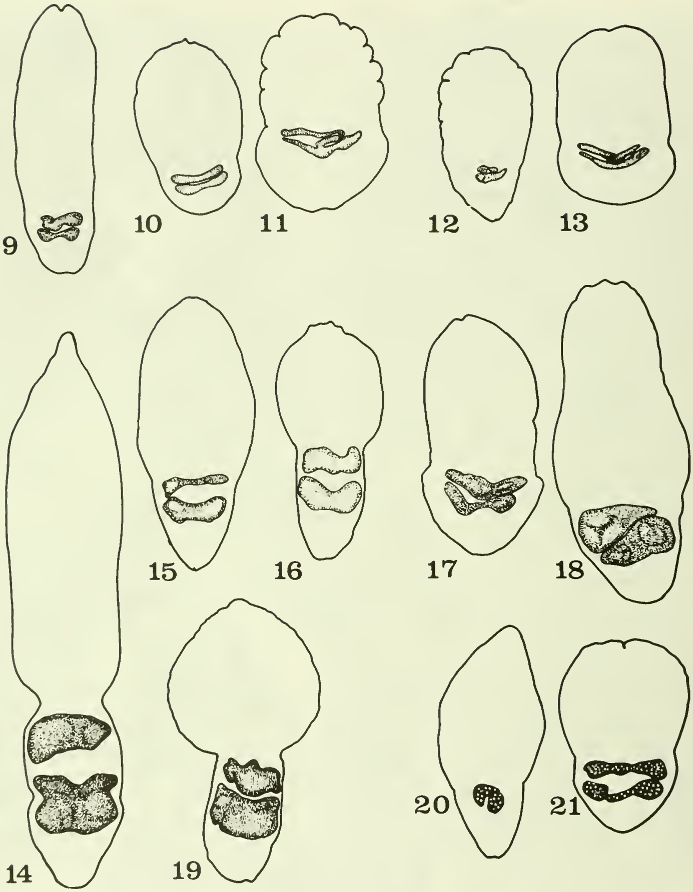






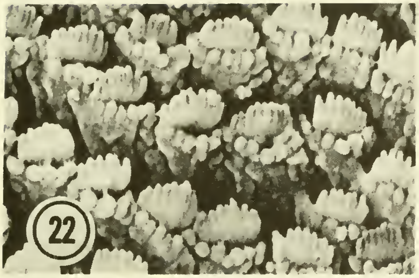


semys picta Note bulblike hindbody and extended; 4, *Didelphis marsupialis* Note slightly reduced forebody; 5, *Felis catus* Note large forebody; 6, *Larus argentatus* Note well-developed forebody and hindbody; 7, *Meriones unguiculatus* Note reduced forebody; 8, *Gallus domesticus* Note reduced forebody.



Figs. 9–21. Outline drawings of adult *P. minimum* from amphibian (Figs. 9–11), reptilian (Figs. 12–13), avian (Figs. 14–16, 19), and mammalian (Figs. 17–18, 20–21). All specimens 72 hours old (Scale: 1 inch = 0.1 mm). Hosts are: 9, *Ambystoma tigrinum;* 10, *Bufo americanus;* 11, *Rana pipiens;* 12, *Thamnophis radix*; 13, *Chrysemys picta;* 14, *Larus argentatus;* 15, *Columba livia;* 16, *Zenaidura macroura;* 17, *Meriones unguiculatus;* 18, *Didelphis marsupialis;* 19, *Ardea heriodias;* 20, *Canis familiaris;* 21, *Felis catus.*

Figs. 22–29. Morphological modification of the tegument of *P. minimum* due to influences of various vertebrate hosts. Figs. 22–25 from an area lateral to and between the acetabulum and holdfast organ. Figs. 26–29 from an area of the dorsal hindbody (Scale: X = 30,000). Hosts are: 22, *Ambystoma tigrinum* (Note the complex nature of the tegumental spines and surrounding tegumental surface); 23, *Meriones unguiculatus* (Note similarity to Fig. 22 with some loss of complexity of tegumental spines and surface); 24, *Chrysemys picta* (Note that tegumental spines have been greatly reduced and are joined to the tegument by a netlike or weblike process); 25, *Iguana iguana* (Note the reduction of tegumental spine serration and surface tegument); 26, *Chrysemys picta;* 27, *Bufo americanus;* 28, *Rana pipiens;* 29, *Ambystoma tigrinum.*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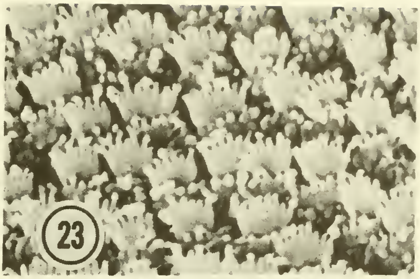
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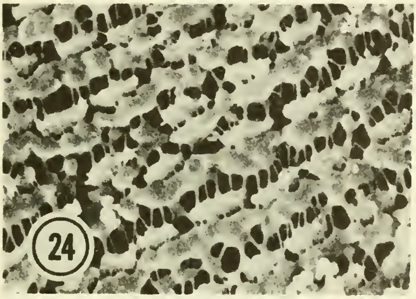
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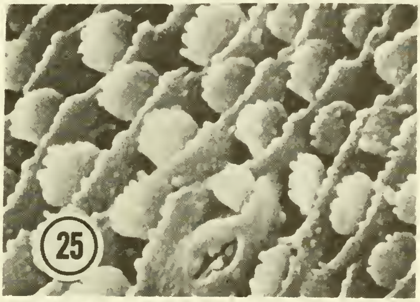
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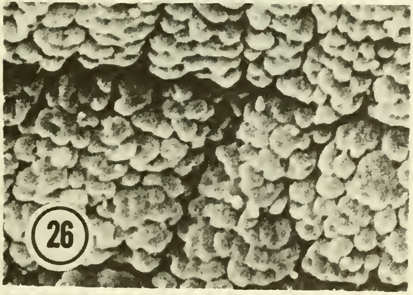
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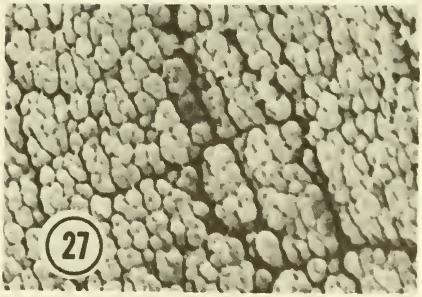
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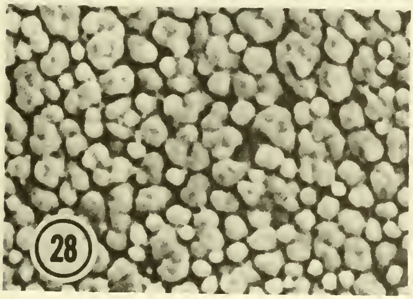
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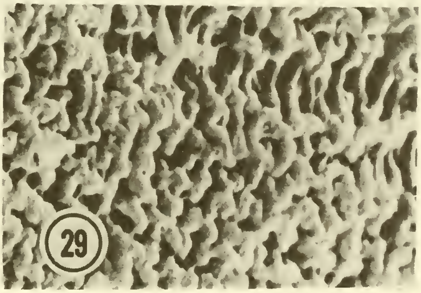
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tion: (1) an area lateral to and equidistant between the acetabulum and holdfast (Figs. 22–25) and (2) a middorsal area on the hindbody (Figs. 26–29). Although no phylogenetic relationships or trends could be discerned, tegumental spination of the ventral forebody surface was reduced from the normal complex structure (Fig. 22). Normal spines are large with serrated margins and are surrounded by tegument containing many surface modifications (Figs. 22–23). In specimens collected from *Chrysemys picta*, spines were so reduced that only a netlike or weblike surface area remained. Such greatly reduced spines are connected to one another as well as to the underlying tegument by filamentous strands (Fig. 24). Tegumental spines examined from most specimens recovered from vertebrate hosts were reduced when compared to others which were more highly developed. There is no apparent relationship between the class of host and complexity of tegumental spine structure. A typical example of a reduced tegumental spine can be found in Figs. 23 and 25, taken from *Iguana iguana* and *Meriones unguiculatus*, respectively.

On the middorsal hindbody of *P. minimum*, the tegument shows some surface modification ranging from a folded appearance (Figs. 26 and 27) (*Chrysemys picta* and *Bufo americanus*) to one in which bleblike modifications of the tegumental surface predominate (Fig. 28) (*Rana pipiens*). A tegument consisting of irregular ridges (Fig. 29) is also common among worms developed within amphibian hosts. Morphological modification of the tegument and associated surface structures are independent of the class of host used for experimental development of the adult *P. minimum*.

Acknowledgments

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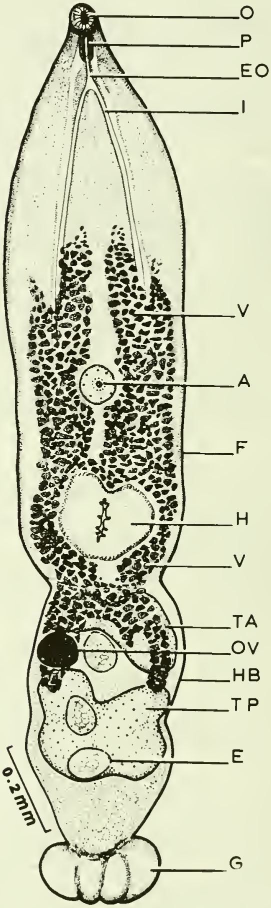

Fig. 30. Diagram of adult *P. minimum* from the gull (*Larus argentatus*) depicting major organs undergoing morphological variation: A—acetabulum; E—egg; EO—esophagus; F—forebody; G— genital bursa; H—holdfast organ; HB—Hindbody; I—intestinal cecum; O—oral sucker; OV—ovary; P—pharynx; TA—anterior testis; TP—posterior testis; V—vitellaria.

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THE SUBFAMILY ANOMIOPSYLLINAE (HYSTRICHOPSYLLIDAE: SIPHONAPTERA). I. A REVISION OF THE GENUS *ANOMIOPSYLLUS* BAKER[1,2]

A. M. Barnes, [3] V. J. Tipton, [4] and J. A. Wildie[4]

ABSTRACT.— In this taxonomic revision of the Nearctic flea genus *Anomiopsyllus* Baker morphological characters, phylogeny, affinities with other genera in the subfamily Anomiopsyllinae, evolutionary adaptations, geographic distribution, ecological parameters, and host preferences are discussed. Characters primarily associated with the male genitalia, in particular the number and placement of spiniforms on the movable process (finger) of the clasper, are used for species discrimination. A key to the males of the 15 species and subspecies is provided, including illustrations of both males and females.

The Nearctic genus *Anomiopsyllus* Baker is a group of small, eyeless fleas associated primarily with wood rats of the genus *Neotoma* and usually found in their nests. These fleas are characterized by the extreme reduction in the number of setae and spiny structures common to most Siphonaptera, and by the reduction and displacement of certain skeletal structures which presumably strengthen the thorax for jumping. These anatomical modifications are carried further in the genus *Anomiopsyllus* than in any other flea genus and reflect a high degree of adaptation to the nest environment.

The genus was proposed by Baker (1904) to include *Typhlopsylla nudatus* Baker, 1898. The subfamily Anomiopsyllinae was established by Baker (1905) to include *Anomiopsyllus*, which was then thought to be phylogenetically isolated and without near relatives. Since Baker's description of *nudatus*, 11 additional *Anomiopsyllus* species have been described, of which *californicus* Baker has been synonomized (Jordan and Rothschild 1915) and *congruens* Stewart has been reduced to a subspecific rank (Hopkins 1952). Traub and Tipton (1951) gave an account of the relationships of the genera within the subfamily Anomiopsyllinae, using characters found in females. Hopkins and Rothschild (1962) reviewed the seven known species and presented keys classifying all males and some females (three species and one subspecies).

While the genus has been treated adequately so far as its placement among the higher taxa is concerned, very little is known of the distribution, geographical variation, biology, or ecology of any of the species. No taxonomic evaluation using all available specimens has been made for any of the species, nor have the intrageneric relationships been analyzed. The primary purpose of this paper is to provide a taxonomic and systematic evaluation of the genus and the member species on the basis of morphological, geographical, and ecological data available from slide-mounted specimens. Distribution, host-parasite relationships, and phylogenetic relationships are also discussed.

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Gratitude and deep appreciation are due Dr. Deane P. Furman, under whose direction the original Ph.D. studies of the senior author were conducted, and to Dr. E. Gor-

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[1] This paper is based on part of an original dissertation completed by the senior author at the University of California, Berkeley, in 1963. It has been modified and updated to include all known species of *Anomiopsyllus*.

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HOST-PARASITE RELATIONSHIPS

Species of *Anomiopsyllus* are most frequently associated with wood rats of the genus *Neotoma*; however, they have been collected occasionally from many ground-dwelling rodents, including species of *Peromyscus*, *Dipodomys*, and *Spermophilus*. There are currently three species of *Anomiopsyllus* that have not yet been associated with *Neotoma: A. oaxacae* Barnes, in which the single specimen was taken from *Baiomys musculus; A. traubi* Barrera, which is known only from a "rodent's nest"; and *A. martini* Holland, which was described from *Sciurus aberti*, a squirrel.

The rodent genus *Neotoma* Say and Ord is widely distributed in North America. The species are normally restricted to a given type of habitat varying from low, dry deserts or humid jungles to rocky slopes above the timberline (Hall and Kelson 1959). Geographical distribution of this genus ranges from Honduras and Nicaragua in Central America to British Columbia in Canada and from California east to New York and Florida in the United States.

There are 22 known species of *Neotoma* comprising 114 taxa on the species and subspecies level. Most flea species of the genus *Anomiopsyllus* are associated with wood rats, and most occur in the arid southwestern United States and Mexico where the average rainfall does not exceed 76 cm. The temperatures in these areas undergo great daily fluctuations and are generally quite high. Nest fleas are somewhat protected from ambient fluctuations because the temperature and humidity in the nest remain at a fairly constant level. Under these circumstances a nest environment may provide some selective advantages over a host environment inasmuch as a host may be away from the nest for long periods of time foraging for food and, thus, the fleas on the host would be exposed to environmental fluctuations.

DISTRIBUTION OF THE GENUS

Anomiopsyllus is exclusively Nearctic, and species have been collected in a geographical area bounded by Banff, Alberta, Canada, on the north (*A. montanus* Collins) and the state of Oaxaca, Mexico, on the south (*A. oaxacae* Barnes). *Anomiopsyllus* is restricted in the United States between the coastal range of California on the west (*A. falsicalifornicus* Fox) and the 101st meridian on the east (*A. nudatus hiemalis* Eads and Menzies). No species have been collected east of the Mississippi River, even though species of *Neotoma* do occur in the eastern United States.

GENERIC RELATIONSHIPS

Eopsylla Argyropulo is the only genus in the subfamily which occurs outside the Nearctic realm. *Eopsylla* was included in the tribe Anomiopsyllini by Hopkins and Rothschild (1962) because it is more closely related to the North American genus *Callistopsyllus* Jordan and Rothschild than it is to other Asian genera. Careful collecting in northwestern North America may reveal the presence of taxa which will further substantiate this relationship.

Genera of the Anomiopsyllinae which are exclusively North American include: *Anomiopsyllus, Callistopsyllus, Megarthroglossus* Jordan and Rothschild, *Stenistomera* Rothschild, and *Conorhinopsylla* Stewart. *Callistopsyllus* has the most northern distribution of these genera and is well represented in western Canada by three species (Holland 1949), two of which enter the United States by way of the Sierra-Cascade mountain chain and the Rocky Mountains. *Megarthroglossus* is also represented in Canada and extends as far south as Texas where *M. divisus* (Baker) and *M. bisetis* Jordan and Rothschild have been collected (Mendez 1956). *Conorhinopsylla* is an eastern genus and is not found further west than Kansas.

Mendez (1956) has stated that *Megarthroglossus* is more closely related to *Anomiopsyllus* than any other genus, and affinities have been shown between these genera based on comparative female characters (Traub and Tipton 1951). However, structures of the male genitalia of *Callistopsyllus* are strongly reminiscent of *Anomiopsyllus*, especially with regard to the clasper and its movable process. The articulation of the movable process in *Callistopsyllus deuterus* Jordan is very similar to that of *A. amphibolus* Wagner and *A. montanus*; the process resembles that of *A. amphibolus*, both in shape and in the presence of two spiniforms. The aedeagi of all three genera have much in common. However, the aedeagus of *Anomiopsyllus* is reduced and has no prominent dorsal or subterminal lobes. The affinities of *Conorhinopsylla* and *Stenistomera* with the rest of the Anomiopsyllinae are also borne out by similarities in male genitalia.

Both distributional and morphological evidence indicate that *Anomiopsyllus* is a member of a monophyletic group, and that the genus has evolved in North America from an ancestor common to other members of the Anomiopsyllinae. *Anomiopsyllus* is more closely related to both *Callistopsyllus* and *Megarthroglossus* than to either *Stenistomera* or *Conorhinopsylla*. In all probability, *Anomiopsyllus* has evolved exclusively in North America in conjunction with the Nearctic genus *Neotoma*, its wood rat host.

SKELETAL ANATOMY OF ADULTS

The remarkably reduced nature of some structures in *Anomiopsyllus* has evoked comment from every author discussing the genus, and in two instances (Ewing and Fox 1943, Hubbard 1947) the genus has been included in the Pulicoidea rather than in the Ceratophylloidea where it was rightfully placed by Jordan and Rothschild (1915). The past taxonomic confusion has undoubtedly resulted from loss of the more obvious distinctive characters typical of Ceratophylloidea, which has brought about a superficial resemblance of *Anomiopsyllus* and the Pulicoidea.

The outstanding features of *Anomiopsyllus* anatomy include complete eyelessness, an extreme reduction in number of setae and spines, extensive loss and fusion of structures in the metathorax, and loss of structures in both meso- and metacoxae. In contrast to the highly modified nature of the thorax, the abdominal segments are only moderately specialized, though marked by loss of some structures in the male genitalia. Of these characters, eyelessness has arisen in a number of widely separated genera and seems to be associated with nest dwellers (Traub 1953).

Reduction in setation in Siphonaptera has been carried to its greatest extreme in *Anomiopsyllus*. Loss of setae and of important spines undoubtedly has great adaptive as well as taxonomic significance. The adaptive significance of such losses is not clear because several highly successful nest fleas which are in some respects as specialized as *Anomiopsyllus* (e.g. *Stenistomera*) have gone in the opposite direction by developing numerous large setae.

In the following section, the more fundamental aspects of *Anomiopsyllus* anatomy are emphasized, especially those in which the genus differs from its relatives and those which would seem to have clear adaptive significance. Snodgrass (1946) has dealt extensively with the skeletal anatomy of fleas; his terminology and interpretations are used here as a basis of comparison.

HEAD

Fig. 1

The head capsule is oval in shape, but its outline is broken anteriorly by a well-defined clypeal tubercle. There is no interantennal suture. The eyes are completely lacking, as in *Callistopsyllus*; the allied *Megarthroglossus* has vestigial eyes.

The degree of sexual dimorphism in antennal size and shape is striking. The small, oval antennae of the female do not reach the prosternum. The male antennae are greatly lengthened with their bases higher up on the head capsule and their apices extending back upon the prosternosome on which the antennal fossae are continued. Though deep, the antennal fossae as seen in a posterior view of the head capsule do not meet in the interior of the head capsule, nor are they connected by a trabeculum.

The mouthparts bear no structures not duplicated elsewhere in Siphonaptera. The extended members are long in proportion to the remainder of the flea and reach the trochanter of the procoxae. The labial palpi are 4-segmented, and the stylets are armed their full length with minute, laterally placed nodules. The epipharyngeal stylet is completely unarmed, as illustrated by Snodgrass (1946) for *Opisodasys* Jordan, and is unlike those of *Hystrichopsylla* Taschenberg and others which bear teeth.

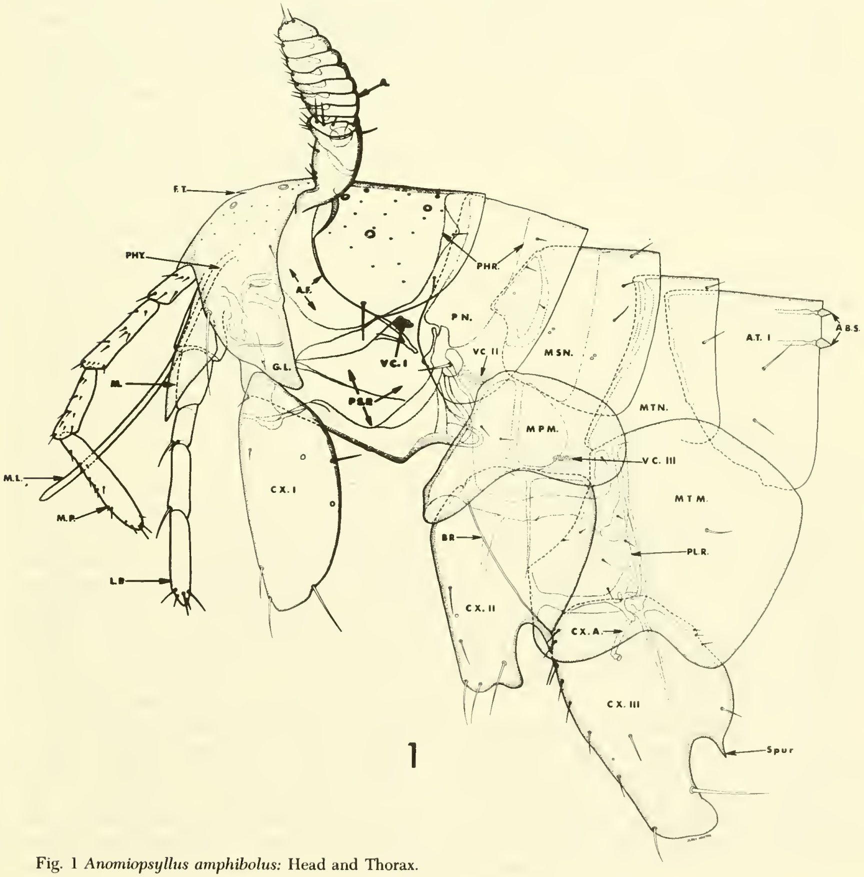


Fig. 1 *Anomiopsyllus amphibolus:* Head and Thorax.

The anterior tentorial arms remain complete and extend from a point near the tentorial bridge to connect anteriorly near the genae. Snodgrass suggested that these arms are in reality the dorsal tentorial arms since true anterior arms arise in the clypeal area. The completeness of these arms and lack of a trabeculum centralis are considered by Johnson (1957) to be primitive characters associated with the Hystrichopsyllidae. In the Ceratophyllidae, the anterior arms are in the process of being lost and replaced by the trabeculum.

In its remarkable antennal sexual dimorphism, *Anomiopsyllus* is highly advanced within the Hystrichopsyllidae, in which the more primitive members show little difference in this regard between the male and female. Within the Anomiopsyllinae all genera show some degree of sexual dimorphism, but of the genera examined *Anomiopsyllus* and *Callistopsyllus* show the greatest antennal enlargement.

THORAX

Fig. 1

Structurally, the thorax is characterized by the total lack of the pleural arch and an extreme degree of fusion in the metathoracic segments. The pronotal comb is absent, and setae are reduced both in number and size.

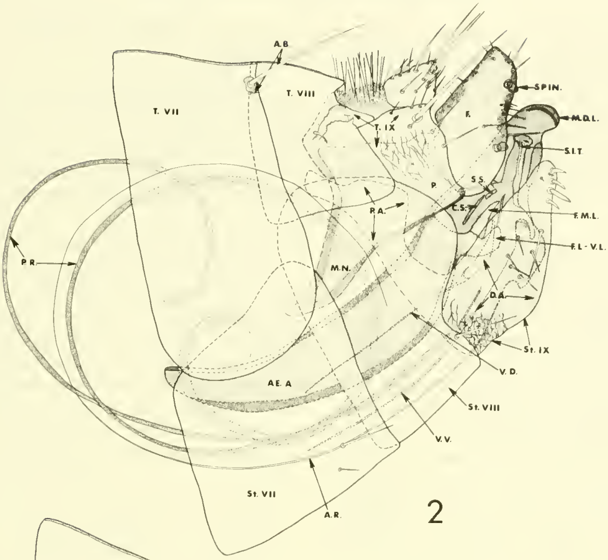
The prothorax, aside from the absence of the pronotal comb, is not remarkable. The fused pleurosternal plate is not divided into the proepisternum and proepimere by a ridge as in *Hystrichopsylla*. The ventral margin of this plate is straight with the dorsal margin sinuously downcurving caudally; thus, the plate is broader anteriorly than posteriorly. The caudal margin of the free flange of the pleurosternum is relatively straight except for a small, sharp, median triangular projection. The pronotum is a simple, collarlike sclerite.

There is considerable disagreement among authors concerning the structure of the sternal and pleural areas of the meso- and metathorax and of the lateral notal and episternal areas of the metathorax. Snodgrass (1946) considered the sternum to consist of a narrow strip lying between the coxae and fused with the episternum anteriorly, leaving the posterior portion of the sternum as a free arm. Jordan (quoted in Hopkins and Rothschild 1953) considered the sternum to have lateral elements fused to the episternum. This divergence in viewpoint confuses terminology: the episternum of Snodgrass is considered the sternum (at least in part) by Jordan; the lateral metanotal area of Snodgrass is considered the episternum by Jordan.

Johnson (1957) follows the interpretation of Snodgrass, whose terminology is used here, and presents additional evidence for its support. She points out that the ventral margin of the episternum in both the meso- and metathorax ends in a free flange and that the sterna are entirely separate from the episterna except where fused anteriorly. The free flanges of the episterna appear not only to extend below the sterna, but also to overlap a portion of the coxae.

The mesothorax of *Anomiopsyllus* is relatively unmodified (Fig. 1). The notum is simple with the anterior phragma large and prominent in slide-mounted specimens. It is marked by the complete loss of internal pseudosetae beneath the mesonotal collar. These pseudosetae are found in other anomiopsyllines and differentiate the Ceratophylloidea from Pulicoidea. The mesepisternum and mesepimere are separated by a strong vertical pleural rod, firmly attached at both ends. This rod supports the pleural articulating sclerites of the coxa. The ventral margin of the mesepisternum curves downward and anteriorly from the base of the pleural rod, forming a free flange slightly overlapping the coxa and fusing anteriorly with the sternum. The ventral margin of the mesepimere is relatively straight. The mesepimere forms a free caudal flange,slightly overlapping the metepisternum near the point of attachment of the third link-plate or vinculum. Dorsally, it slightly overlaps the ventral edge of the mesonotum except at the anteriormost corner.

The metathorax of *Anomiopsyllus* (and all other Anomiopsyllinae) is marked by extreme fusion and a rather radical displacement of parts. The net effect is anterior fusion of the notum with the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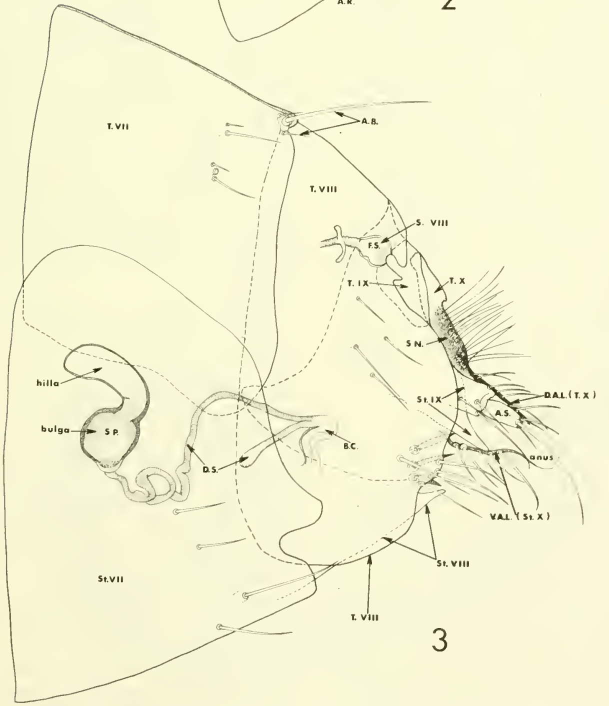
2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bulga
S.P.
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D.S.
anus
V.A.L. (St. X)
St. VIII
St. VII
T. VIII

3

Figs. 2-3. *Anomiopsyllus amphibolus:* 2, male terminalia; 3, female terminalia.

metepisternum, loss of the lateral metanotal area, and loss of the pleural arch. These complex phenomena have been subject to some discussion by taxonomists, particularly Johnson (1957), and warrant further discussion and clarification, especially with regard to the mechanics involved, evolutionary trends, and possible adaptive significance.

In order to understand what has taken place in the metathorax, it is necessary to review the work of Snodgrass (1946), especially with regard to the strengthening rods and lateral metanotal area.

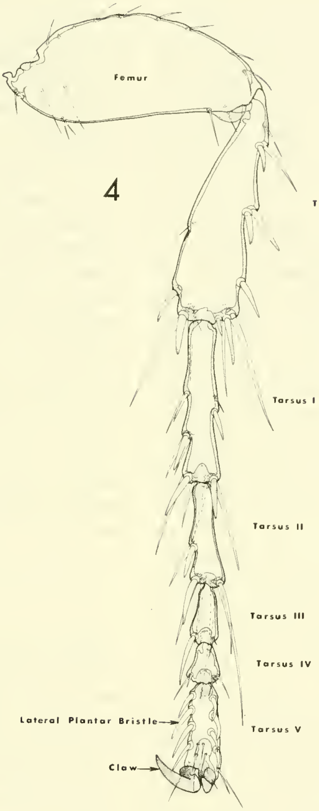
In most fleas, the metanotum is a collar-shaped structure. It normally bears two transverse strengthening ridges, the anterior prephragmal ridge and the more posterior notal ridge. Near the lower end, the transverse notal ridge gives off anteriorly a short longitudinal ridge which usually continues to the anterior edge of the notum where it blends into a marginal thickening continued around the ventral edge of the notal plate. The accessory ridge thus sets off a small, variously shaped ventrolateral area of the metanotum, termed the lateral metanotal area (see Snodgrass, Pl. 8., Figs. K-O; Pl. 9, Figs. A-E). This area normally bears a small but distinct, free marginal flange, but in *Pulex* it is fused with the upper margin of the metepisternum. Contrary to the findings reported by Johnson (1957), *Pulex* still retains the lateral metanotal area: though fused with the metepisternum, it is still set off by the ventrolateral thickening extending from the lower anterior margin to the ventral extension of the notal ridge.

The notal flange normally extends into the pleural area, where it terminates in an oval expansion that overlaps and clasps the upper end of the pleural rod, thus forming the so-called pleural arch (see Snodgrass, 1946: 26, Pl. 9, Figs. C, H-K). The union is a very firm one. Snodgrass states (p. 26): "It is evident, therefore, that this apparent notopleural 'articulation' of the metathorax is for the purpose of solid union along the line of the notal and pleural ridge, and is not for controlled movement. The flexibility of the united ridges allows the pleuron to be twisted somewhat on the notum, but *permits of no swinging* movement in a longitudinal plane."

According to Snodgrass, *Opisodasys* and *Dactylopsylla* Jordan possess a pronounced posterior angulation between the notal flange and the axis of the pleural ridge. This condition applies in *Orchopeas* Jordan and most ceratophyllids. In these fleas, the pleural ridge has moved anteriorly to the line of the notal flange and is fused strongly to its angled ventral extension.

In *Anomiopsyllus* and allies, much more radical changes have taken place. In *Anomiopsyllus, Megarthroglossus, Callistopsyllus,* and *Stenistomera*, the notal ridge is strongly reduced in thickness and extent and the lower portion has disappeared above the notal margin. The accessory ridge is still present; its identity is established by the attachment of the link-plate or vinculum at its anterior end (Fig. 1, VC. II). This ridge is strongly developed anteriorly, but fades posteriorly to varying degrees in the anomiopsyllines examined, and does not meet the ventral remnant of the notal ridge. The ventral extension of the notal ridge is apparently gone. The long metapleural rod has been displaced anteriorly and is apparently completely fused with the accessory ridge. There is no sign of a pleural arch. Along with this, the metepisternum and metanotum are completely fused, and in *Anomiopsyllus* there is no vestige of the lateral metanotal area.

A clue to what has happened is present in *Megarthroglossus*, and perhaps in *Stenistomera* and *Callistopsyllus*. In *Megarthroglossus* a small thickening leads anteriorly from the upper portion of the pleural rod, but ends before it reaches the anterior margin of the segment. Its position suggests that it represents the vestigial ventral thickening of the lateral metanotal area. A similar thickening exists in the other genera, but leads posteriorly from the anterior margin. In *Stenistomera* the thickening is short and knoblike and in *Callistopsyllus* it is longer. If the structure in *Megarthroglossus* is indeed, as suggested, part of the "pleural rod," it must represent the ventral portion of the notal flange, which has completely fused with the pleural rod. The notal flange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Tarsus V
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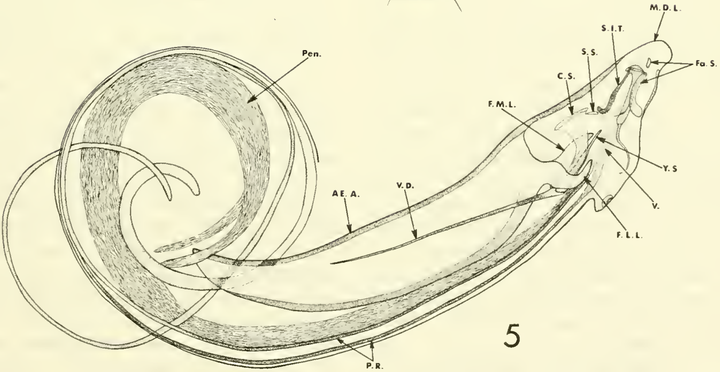
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Figs. 4-5. *Anomiopsyllus amphibolus:* 4, metathoracic leg; 5, aedeagus.

has lost its direct connection with the notal ridge proper and has been displaced anteriorly with the pleural rod. This would be correct, since the ventral thickening of the lateral metanotal area always connects with the ventral extension of the notal ridge in those fleas that possess the lateral metanotal area. In the ceratophyllid genus, *Orchopeas*, and perhaps others, we see a forward angulation of the ventral end of the notal ridge and an anterior displacement of the pleural rod, but the elements essential to the pleural arch are present and highly developed. In *Anomiopsyllus* and allies these structures have been entirely lost or have lost identity by fusion.

Johnson (1957:8) has offered an explanation of the adaptive significance of the loss of the lateral metanotal area and the pleural arch. According to her, the pleural arch serves as a strengthening device which acts as a "cushion" in jumping. Since *Anomiopsyllus* is a "nest flea" and consequently a "poor jumper," the pleural arch is no longer necessary. She explains the means by which it was lost as "... probably loss due to lack of selection against any mutation tending toward reduction of the pleural arch which, if my premise is correct, is mainly an aid in jumping."

The negative view that such a radical change involving major structures has arisen by mutations in the absence of selection pressures is difficult to accept. Such phenomena undoubtedly occur in isolated island populations where the gene pool is small and selection pressure slight, but they must be exceedingly rare in any continental group. In a rigorous continental environment, one would not expect mutations to survive in the absence of some positive selective advantage to the mutant. One must postulate that any such radical change would have to offer a positive selective advantage to be retained. Losses which may take place by mutation in the absence of selection could be termed degenerative evolution. Thus, *Anomiopsyllus* may be dubbed a "degenerative form," a term disapproved of by Johnson (1957:16).

The possible selective advantage of the anterior displacement and fusion of strengthening ridges in the metathorax of anomiopsyllines may be partially clarified by observations of adult fleas in the laboratory under both artificial and near-natural conditions. *Anomiopsyllus* is not a weak jumper. It does not jump at all! *Callistopsyllus*, *Megarthroglossus*, and *Stenistomera* are weak jumpers. This is probably due in part to correlated differences in meso- and metathoracic coxae as well as to changes in the metathorax. This becomes apparent with microscopic observations of flea movements through tangles of nest material. The abdomen of *Anomiopsyllus* is capable of sweeping movement *in the lateral plane* as the flea moves through nest material with a rapid, sinuous movement. Lateral flexibility is not observable in the more rigidly constructed *Hystrichopsylla* and *Atyphloceras* Jordan and Rothschild. Anterior displacement of thoracic ridges and reduction of the notal ridge offer a considerably greater degree of flexibility in the metathorax.

LEGS
Fig. 4

The legs of *Anomiopsyllus* are marked by prominent posteroapical sinuses on both meso- and metacoxae, above which are large subacuminate spurs (Figs. 1, SPUR). The prolegs are not distinctive. The mesocoxae possess a complete longitudinal break (Fig. 1, BR.), considered to be an advanced condition. A complete break is also found in *Megarthroglossus*, but not in *Callistopsyllus* or *Stenistomera*. This condition also is found among the Rhadinopsyllinae. In an anterior view, the mesocoxae are seen to fold inward at the break, forming a shield similar to that formed by the procoxae, as described by Snodgrass (1946). The shield is formed by pivoting the procoxae at the pleurocoxal articulations. Snodgrass postulated that the "shield" formed by the procoxae may be useful for forcing between hairs or may be used as a flat base for feeding. The second "shield" formed by the mesocoxae in *Anomiopsyllus* and *Megarthroglossus* suggests the former explanation and perhaps is needed to cope with the greater heterogeneity and density of nest material rather than hairs on the host.

In *Anomiopsyllus* and other anomiopsyllines, the exterior coxal ridge in both meso- and metacoxae is incomplete. In those fleas examined by Snodgrass (1946), including *Pulex* Linnaeus, *Hystrichopsylla*, *Dactylopsylla*, and *Opisodasys*, and in most other fleas, the ridge is complete and reaches the apex of the coxae. The meso- and metacoxae are articulated mesally to the sternum by a pair of prominent articulating sclerites (Fig. 1, CX. A). The upper mesal coxal surface is membranous, and the articulating sclerites serve as the only rigid connection between sternum and coxae. These sclerites normally articulate with a well-defined socket in the dorsal edge of the mesal sclerotized surface of the coxa. At the point of articulation, the coxa is strengthened by a horizontal thickening and a longitudinal rod extending toward the coxal apex (see Snodgrass 1946) and may or may not reach the apex of the coxa. This structure has been termed the mesal coxal ridge by Snodgrass. In *Anomiopsyllus*, there is no hint of thickening at the point of articulation and the rod is entirely absent. Both thickening and rod are present in the related genera *Callistopsyllus*, *Megarthroglossus*, and *Stenistomera*.

The reduction of the coxal ridge, absence of mesocoxal ridge, and complete mesocoxal break in *Anomiopsyllus* would seem to be further examples of specialization to the nest environment and to walking rather than jumping.

ABDOMEN

The unmodified abdominal segments (I-VI) are not remarkable except for the characteristic reduction in number and size of setae. Terga I and II each bear spinelets at the apical margin, the former usually 2 per side, the latter 1. Each tergum bears a row of thin setae, 3 to 5 on each side, plus 1 very minute guard seta below and anterior to each spiracle. Sterna II to VI are simple, usually bearing two setae ventrally, the upper one usually the longer.

MODIFIED ABDOMINAL SEGMENTS OF MALES (Fig. 3): Segment VII is the first modified segment. The tergum bears one long antepygidial seta which is not reduced or altered in shape. Sternum VII is not modified differently from preceding sternal segments. Sternum VIII is expanded posteriorly and dorsally to serve as the chief ventrolateral shield about the genitalia and differs markedly from the more anterior segments. The tergum is marked at the posterior margin by rather prominent setigerous grooves containing the spiracles below which it expands caudally to serve as the main dorsolateral shield for the genitalia. It is comparatively shallow, descending ventrally only about half the distance of the preceding terga. Sternum VIII closely resembles that of the other Anomiopsyllinae by being expanded and ensheathing much of the proximal portion of sternum IX.

Segment IX of males (Fig. 3) is exceedingly modified; included in its structure is the clasping apparatus of the external genitalia. Its tergum is much reduced dorsally and consists of a narrow but complete strap anterior to the pygidium (Figs. 3-4, T. IX). The tergum is continuous with the upper anterior angle of the clasper lobes, very much as noted for *Hystrichopsylla* by Snodgrass (1946). Immediately below and anterior to the tergal strap is a small but strong tergal apodeme, reinforced by thickened bars that join the anterodorsal angles of the large manubria (Figs. 3, MN). The apodeme forms a strong dorsal arch between the manubria at this point from the anterior edge of the dorsal arch. The anterior margin descends downward into the abdominal cavity, then curves dorsally and posteriorly to join the clasper lobe, thus forming a prominent triangular structure.

The tergal clasping apparatus consists of the broadened clasper lobe composed of a more or less dome-shaped fixed process (P) and an articulated movable process (F). The fixed process is usually equipped at or near the apex with a long, heavy bristle projecting over the apex of the movable process (lacking in *A. novomexicanensis*). Invariably, the movable process or "finger" is equipped with heavily pigmented, large spiniform setae on the mesal surface. The number and position of these setae have been used extensively in taxonomy. The posteroventral apex of the clasper lobe below the articulation of the movable process bears the acetabular seta. The articulation of the movable process is on the *inner* surface of the clasper lobe. The socket may be oval or nearly round (as in *nudatus*, *novomexicanensis* and *falsicalifornicus* groups) or linear and nearly vertical (as in the *amphibolus* group).

Sternum IX (Fig. 3) consists of two main components, the proximal and distal arms. Together, in lateral view, they form a prominent V-shaped structure easily seen in slide-mounted specimens. The proximal arms are platelike sclerites, characteristically shaped in some species but variable enough that taxonomic value is limited. In *Anomiopsyllus*, they extend dorsad and anterad almost to the anterodorsal angle of the manubrium. The distal arms form a single troughlike structure from the base to a point 20 to 25 percent of the distance from the apex, after which they separate and are free. The heavily reinforced lateral portions are interconnected by a more lightly sclerotized, distally convex median plate variously adorned by setae. The pattern is characteristic of the species. The apices of the free arms are equipped with large, tacklike setae. Their number and size are of taxonomic value. In some species, there is a lobe which forms a narrow sheath around the angle of the distal arm about three-fourths of its length. In others, this structure is greatly reduced and difficult to see.

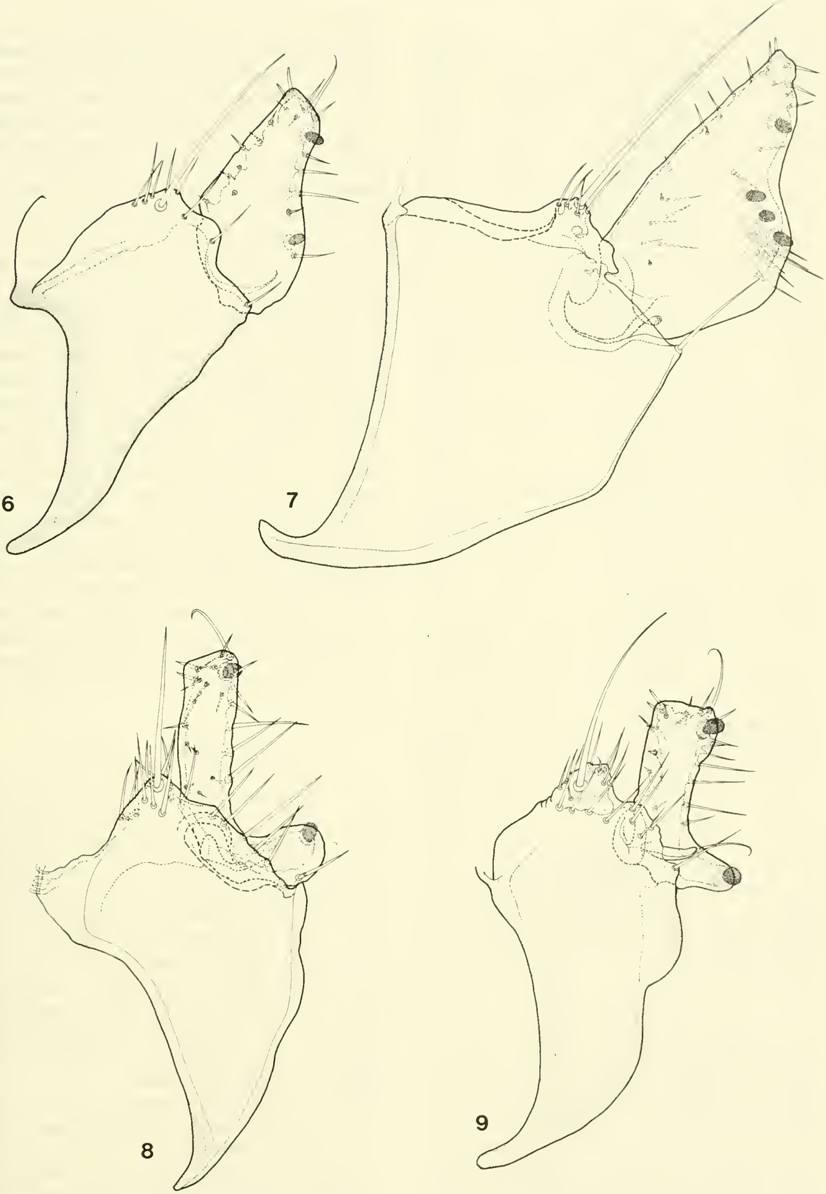
AEDEAGUS (Fig. 5): The aedeagus of *Anomiopsyllus* is simple and basically very similar to that of *Hystrichopsylla dippiei* Rothschild, as described by Snodgrass (1946) and Traub (1950). It is long and narrow. The apodeme is broadly scimitar shaped with a prominent basal constriction or neck. The endchamber is a simple hood opened apically and ventrally. The crochets (CR) are reduced and immovable in the ventrolateral wall. The aedeagal pouch is deep, extending considerably cephalad of the struts. The sclerotized inner tube (S.I.T.) is prominent, tubular, and funnel shaped at the base with a prominent anteroventral spur to which is attached the apodemal rod. The crescent sclerite (C.S.) of *Anomiopsyllus* is prominent and attached to the anterodorsal flange of the tube. Penis rods are long and coiled. There are no specialized lobes present, indicating its primitiveness as compared to ceratophyllids and pulicids.

MODIFIED ABDOMINAL SEGMENTS OF FEMALES (Fig. 2): Tergum VII bears the single, long antepygidial bristle. Sternum VII is marked by a posterior expansion with its margin shaped variously in the several species. The upper margin of sternum VII, as pointed out by Snodgrass (1946), overlaps its tergum (Fig. 2, St. VII).

Segment VIII is exceedingly modified. The tergum consists of two lateral plates narrowly joined dorsally, expanding ventrally and posteriorly to cover most of the genitalia. Its posterior margin near the dorsum contains the deep setigerous grooves of the most posterior spiracle. From that point, it expands posteriorly. The most posterior margin may be straight or lobed (Fig. 2, T VIII), depending on the species. Its usefulness as a taxonomic character is reduced by intraspecific variation. Sternum VIII, as in other fleas, is reduced to a small plate between the two valves of its tergum and functions only as the ventral floor below the genitalia.

Tergum VIII completely encloses the external genital chamber and is guarded at its orifice by a group of very heavy, inward-directed mesal setae. The lateral walls of the genital chamber are heavily sclerotized in *Anomiopsyllus*, apparently forming a channel. The bursa copulatrix is a simple sack at or near the anterior end of the "channel." The bursa, in some species, (notably *novomexicanensis* Williams and Hoff, Fig. 90) has minute areas of sclerotization, and in others it appears as a wholly membranous sack. The spermatheca is simple, with a more or less globular bulga (head) and a curving, broad hilla (tail) without a terminal appendage (Fig. 2).

Segment IX in *Anomiopsyllus* is marked by well-developed tergal plates. As pointed out by Snodgrass (1946: 36), segment IX of most female fleas is virtually obliterated. Those groups retaining well-developed tergal plates on this segment include: *Hys-*



Figs. 6-9. Finger and clasper: 6, *Anomiopsyllus amphibolus*; 7, *A. nidiophilus*; 8, *A. montanus*; 9, *A. sinuatus*.

trichopsylla (Snodgrass 1946); *Ctenopthalmus* Kolenati, 1956; *Parapsylla* (Wagner, 1939); and *Atyphloceras* Jordan and Rothschild, 1915. *Anomiopsyllus* is suggestive of the more primitive hystrichopsyllid genera in the retention of a well-developed tergum IX. These plates consist of teardrop-shaped valves on either side of the pygidium, well rounded dorsally, ventrally, and anteriorly but acute posteriorly with points projecting beyond the anus, below the anal stylets, and outside the anal plate (Fig. 2, 3, T. IX). From the dorsal aspect, the plates appear to be joined anteriorly only by a membranous connective and are completely separated from tergum X by a suture.

Segment X contains the prominent pygidium, the proctiger, and the anus. The pygidium is framed by a narrow, strongly sclerotized ring somewhat open anteriorly but joined by a small plate. It bears 20 (10 per side) sensillial pits (Fig. 2, SN.), though 21 were noted on one specimen of *A. f. congruens* from Placerville, California. The number of sensillia is used as a key character by Hopkins and Rothschild (1956) to separate Pulicoidea from Ceratophylloidea. According to them, pulicoids bear 8 to 14 sensillial pits per side and ceratophylloids sometimes bear 14 but usually bear 16 or more. The reduced number of these pits in *Anomiopsyllus*, a definite ceratophylloid in other respects, is interpreted here as an example of convergence through loss and does not indicate pulicoid affinities. The proctiger (Fig. 2, DAL.) is prominent and well endowed with strong setae. The anal stylets are simple and equipped with one long terminal seta and one or two minute subterminal setae.

DISCUSSION

The skeletal anatomy of *Anomiopsyllus* is most marked for its extreme reduction of parts and small size. This reduction has been accompanied in *Anomiopsyllus* by the loss of a number of behavioral characteristics common to fleas, particularly the ability to jump. Undoubtedly these reductions are adaptations to its role as a nest flea, with *Anomiopsyllus* progressing further than any other flea group. The loss of the pleural arch and the moving forward of the pleural rod reduce the mobility of *Anomiopsyllus* as far as jumping is concerned, but probably enable the flea to move through heterogeneous nest material at a more rapid rate. Modifications of the mesocoxae probably also serve this purpose.

With respect to both male and female modified abdominal segments, *Anomiopsyllus* has retained the basic structure of its more primitive relatives in the Hystrichopsyllidae. The aedeagus, for example is far less complex than that of any ceratophyllid or pulicid, and less complex than that of the other Anomiopsyllinae, including *Callistopsyllus* and *Megarthroglossus*, to which it is most closely related. Nevertheless, the relationships of the aedeagus of *Anomiopsyllus* to those of its hystrichopsyllid relatives are made clear by comparison with that of *Hystrichopsylla*. In the female, retention of the ninth tergal plates further links *Anomiopsyllus* to its more primitive hystrichopsyllid relatives. The reduction in the total number of sensillial pits on the pygidium represents specialization, probably accompanying overall reduction in size.

CHARACTERS USED IN THE STUDY

The differences between *Anomiopsyllus* species and, to an even greater extent, between subspecies are found almost entirely in the male external genitalia. Few tenable characters are available in females. For the most part, differences in configuration of sternum VII of females serve only to separate species groups. Configuration of the posterior margin of tergum VII used by Hopkins and Rothschild (1962) to separate species in their key does not hold when long series are studied, though trends may exist in any given population.

In males, particular attention has been given structures of the ninth abdominal segment, which is modified to form the clasping apparatus of the external genitalia. The shapes of the movable and immovable processes are somewhat variable within species, but are nevertheless stable enough to constitute good species characters. Consistent differences in these structures also serve as species group characters as does the structure of the articulation of the movable process. Arrangement and number of setae of both the movable and immovable processes of the clasper serve as species and subspecies characters. In some of the species one of the prominent spiniforms of the movable process seems to be in the process of being lost and is absent in some specimens. Differences in the shape and setation of the distal arm of sternum IX are useful at the subspecific level and more so at the specific level. The general shape of the proximal arms of sternum IX is useful as a secondary character at the species level, but varies a great deal in detail and is not usable in determining subspecies. Among several subspecies the distance between prominent spiniform setae has proven to correlate well with other characters, including geographic distribution. The aedeagus varies less than do other structures of the genitalia; nevetheless, some variation does occur in configuration of the dorsal margin and in dimensions. These are of some use at the species level.

LIST OF ABBREVIATIONS

A.	Antennae
A.F.	Antennal fossa
AE.A.	Aedeagus apodeme
A.B.	Antepygidial bristles
A.R.	Apodemal rod
A.S.	Anal stylet
AB.S.	Abdominal spinelets
A.T.I	Abdominal tergum I
B.C.	Bursa copulatrix
C.S.	Crescent sclerite
CX.A.	Coxal anticulating rod
CX. I	Coxa I (Pro)
CX. II	Coxa II (Meso)
CX. III	Coxa III (Meta)
D.A.	Distal arm of Sternum IX
D.A.L. (T.X.)	Dorsal anal lobe (Tergum X)
D.S.	Duct of spermatheca (Ductus seminalis)
F.	Finger (movable process) of clasper
F.L.L.	Fulcral lateroventral lobe
F.M.L.	Fulcral median lobe
FO.S.	Ford sclerite
F.S.	Fossa spiracular
F.T.	Frontal tubercle
G.L.	Genal lobe
L.P.	Labial palp
M.D.L.	Median distal lobe of aedeagus
MSN.	Mesonotum
MTN.	Metenotum
M.L.	Maxillary lacinia
MN.	Manubrium
M.P.	Maxillary palp
MPM.	Mesepimeron
MTM.	Metepimere
M.	Maxilla
P.	Process (immovable) of clasper
P.A.	Proximal arm of Sternum IX
PHR.	Phragma
PHY.	Pharnyx
PN.	Pronotum
PEN.	Penis
P.R.	Penis rods
PL.R.	Pleural rod
PSP.	Pleurosternal plate
SP.	Spermatheca
SN.	Sensillium
S.I.T.	Scleritized inner tube
SPIN.	Spiniform
S.S.	Satellite sclerite
ST. VII	Sternum VII
ST. VIII	Sternum VIII
ST. IX	Sternum IX
T. VII	Tergum VII
T. VIII	Tergum VIII
T. IX	Tergum IX
V.	Vesicle
V.A.L. (St. X)	Ventral anal lobe (Sternum X)
VC. I	Vinculum I (Link-plate I)
VC. II	Vinculum II (Link-plate II)
V.D.	Virga dorsalis
Y.S.	"Y" sclerite

SYSTEMATIC SECTION

Anomiopsyllus Baker

Anomiopsyllus Baker, 1904, Proc. U.S. Nat. Mus. 27: 377 (Type Species: *Typhlopsylla nudata* Baker, 1898.); Oudemans, 1909, Nov. Zool. 16: 157; Jordan and Rothschild, 1915, Ectoparasites 1: 45; Dalla Torre, 1924, Natur. Med. Ver. Innsbruck 39: 17; Ewing, 1929, Manual of Ectoparasites: 162; Jellison and Good, 1942, Index to the literature of Siphonaptera of North America: 21; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500; Costa Lima and Hathaway, 1946, Monogr. Inst. Oswaldo Cruz 4: 522 pp.; Hubbard, 1947, Fleas of western North America: 56, 78; Holland, 1949, Siphonaptera of Canada: 96; Eads and Menzies, 1950, Fleas of Texas; Anon., 1950 (a & b), Public Hlth. Repts. 65: 454, 526; Traub and Tipton, 1951, J. Wash. Acad. Sci. 41: 267-268; Wiseman, 1955, Univ. Wyo. Publ. 19: 28 pp.; Finley, 1958, Univ. Kans. Publ. Mus. Nat. Hist. 10: 213-522; Parker and Howell, 1959, J. Parasitol. 45(6): 507-604; Stark, 1959, Siphonaptera of Utah; Vargas, 1960 Med. Rev. Mexicana 40 (849): 1; Kartman et al., 1960, Zoon Res. 1(1): 178; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 392; Holland, 1965, Canadian Ent. 97: 1051-1058; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Tipton and Mendez, 1968, Pacific Insects 10(1): 179-182; Beck and Allred, 1966, Brigham Young Univ. Sci. Bull., Biol. Ser. 7(2): 13; Stark and Kinney, 1969, J. Med. Ent. 6(3): 290; Pratt and Stark, 1973, DHEW Publication 74-8267: 11; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsylla (sic): Augustson and Durham, 1961, Bull. South. Calif. Acad. Sci 60(2): 100.

Anomiopsyllus is immediately separable from other Anomiopsyllinae by extreme reduction in number and size of setae, lack of a pleural arch, and absence of a pronotal comb and from *Eopsylla* by the lack of internal mesonotal setae (Hopkins and Rothschild 1962).

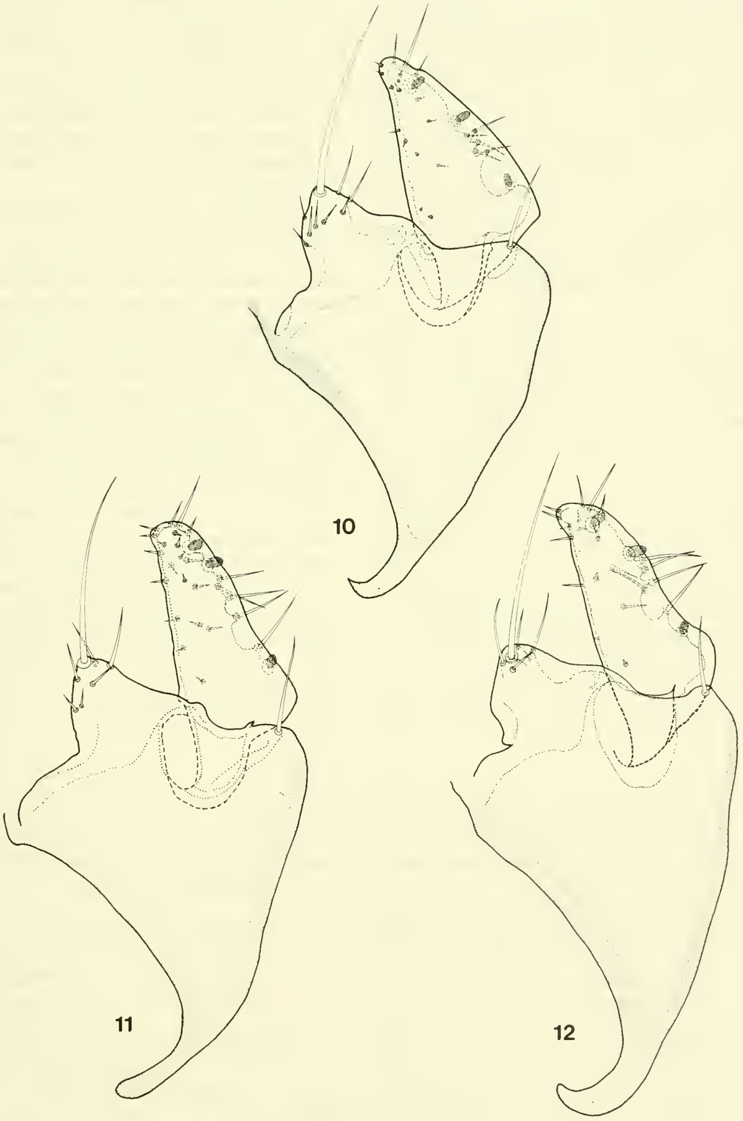
HEAD.— Rounded anteriorly, clypeal tubercle present, prominent; eyes absent; trabecula centralis absent; labial and maxillary palpi 4-segmented, reaching to or slightly beyond protrochanter; terminal segment of labial palpi not markedly asymmetrical nor greatly longer than other segments; maxillae acutely triangular, somewhat convex anteriorly; concave posteriorly, genal lobe broadly rounded, short. Antennae of male much enlarged, antennal fossae of males beginning almost at dorsal margin of head, connected dorsally by a falx; second antennal segment not overlapping base of third; antennal setation sparse, short, setae of female second antennal segment only one-fourth length of clava. Frons with one row of setae; occiput with a row of minute setae; antennal fossa with several setae along posterior margin.

THORAX.— Pronotal comb absent, pseudosetae absent. Pleural arch absent. Metepimeron partially fused with metanotum, latter with a small, free posteroventral flange. Metepisternum completely fused with metepimeron and anterior portion of metasternum. Posterior margin of mesocoxa and metacoxa deeply emarginate preapically, forming a deep sinus and sharp preapical spur, mesocoxa with a prominent longitudinal break from anterior base to preapical posterior sinus. Coxae, femora, and tibiae with few or no lateral setae, procoxae with row of long, thin setae on posterior margin. Femora and tibiae with weak posterior marginal setae, meso- and metafemora and tibiae with few very weak anterior marginal setae. Tarsi with four lateral pairs of plantar bristles, the basal pair moved ventrally on the pro- and mesotarsi.

ABDOMEN.— Terga with one row of weak setae; tergum I with two to four apical spinelets; tergum II with one or two. Abdominal sterna each with two slender, ventral submarginal setae. One antepygidial bristle in both sexes.

FEMALE.— Tergum VIII posterior margin sloping posteroventrally, then ventrally to enclose the genitalia. Genital chamber marked by heavily pigmented area on tergum VIII, its gonotreme protected by four to six heavy, distomesad setae, forming an "ovipositor." Tergum IX large, broadly curving laterad around pygidium and proctiger, tapering to an acute point posterolaterad near anal stylet. Anal stylet approximately 2.0 to 2.5 times as long as broad, with long, slender, curving terminal seta and one minute preapical, subdorsal seta. Anal plate broad at base, dorsal margin linear, ventral margin gently curving to point.

MALE.— Tergum IX narrow but entire dorsally with a well-developed tergal apodeme forming clasper lobe laterally. Clasper and manubrium roughly triangular, descending deeply into abdominal cavity; fixed process well developed; movable process variable, always with two to four heavy, pigmented, distomesad spiniform setae. Sternum IX V-shaped, proximal arm extending anterodorsally into body cavity, distal arm extending posterodorsally to form a posteroventral sheath about external genitalia, fitted distally with two free lobes armed at subapical posterior margin with modified setae. Aedeagus large, apodeme broadly scimitar shaped, bearing a weak terminal appendage. Apodemal neck present and well developed. Endchamber without well-developed, specialized lobes or with none, covered by a simple, weakly sclerotized hood, open apically and ventrally, extending from apex cephalad to a point anterior to



Figs. 10-12. Finger and clasper: 10, *A. nudatus hiemalis*; 11, *A. nudatus nudatus*; 12, *A. nudatus mexicanus*.

aedeagal struts, then curving dorsally and anteriorly as lateral lobes of aedeagal apodeme. Aedeagal pouch arising below trough, extending distally and dorsally toward base of sclerotized inner tube, latter strongly sclerotized, broad at base, ventral margin curving ventrally and cephally; narrowing to a well-developed tube posterally, apex without auxiliary sclerites. Crescent sclerite (C.S.) present. Crochets represented by very small, internal, unarticulated plates at ventral apex of endchamber. Penis rods long, coiled. Aedeagal apodemal rods present, well sclerotized. Ventral intramural rod present.

The species, though closely related, may be separated into five species groups based on characters in the male genitalia. The characters used in the grouping are: (1) number of spiniforms on finger of clasper and (2) position of spiniforms on distal or proximal portion of finger curve in either vertical or oblique rows. The grouping, though artificial, may give an indication as to the phylogeny of this genus. The five groups are:

1. Spiniforms: 1 distal, 1 proximal: *amphibolus, montanus,* and *sinuatus.*
2. Spiniforms: 2 distal, 1 proximal: *nudatus nudatus, n. mexicanus,* and *n. hiemalis.*
3. Spiniforms: 3 distal, 1 proximal: (vertical row) *martini* and *walkeri*; (oblique row) *falsicalifornicus falsicalifornicus* and *f. congruens* (*f. falsicalifornicus* has apparently lost the proximal spiniform in its evolution).
4. Spiniforms: 3 distal: *novomexicanensis, traubi, oaxacae,* and *durangoensis* (in *durangoensis* one of the distal spiniforms has apparently been lost in its evolution).
5. Spiniforms: 1 distal, 3 proximal: *nidiophilus.*

The most widely distributed group of this genus is represented by *A. amphibolus* and *A. montanus* in the north and *A. sinuatus* in the south. The northern species are most closely related to the genus *Callistopsyllus.* The *nudatus* group, represented by three subspecies, is distributed primarily on the Colorado Plateau in the Sonoran Desert, which extends into Mexico. The distribution of the *falsicalifornicus* group is coastal or subcoastal in the Pacific region of North America. The distribution of *nidiophilus, traubi,* and *oaxacae* is limited to Mexico. *Anomiopsyllus princei* has been collected only from New Mexico and *martini* only from Mexico; however, both of these species have been collected only from *Sciurus aberti,* suggesting that they could be the same species. Further collecting is needed to determine their relationship.

Key to Male *Anomiopsyllus*

1. Finger of clasper with both distal and proximal spiniforms 2
Finger of clasper with only distal spiniforms 11

2(1). Finger with 1 distal and 3 proximal spiniforms .... *nidiophilus*
Finger with 1 or more distal but only 1 proximal spiniform 3

3(2). Finger with 1 distal and 1 proximal spiniform 4
Finger with 2 or 3 distal and 1 proximal spiniform 6

4(3). Finger triangular shaped (Fig. 7) .... *amphibolus*
Finger boomerang shaped (Fig. 8,9) 5

5(4). Finger broad; 3 heavy bristles on apex of St. IX (Fig. 33) .... *sinuatus*
Finger narrow; 4 heavy bristles on apex of St. IX (Fig. 32) .... *montanus*

6(3). Finger with 2 distal and 1 proximal spiniform 7
Finger with 3 distal and 1 proximal spiniform 9

7(6). Distance between distal spiniforms under 20u .... *nudatus nudatus*
Distance between distal spiniforms over 20u 8

8(7). Thin bristle at angle of divergence of St. IX (Fig. 35) .... *nudatus hiemalis*
Thick bristle at angle of divergence of St. IX (Fig. 36) .... *nudatus mexicanus*

9(6). Finger with distal spiniforms in oblique row in relation to posterior margin (Fig. 13) .... *falsicalifornicus congruens*
Finger with distal spiniforms in vertical row in relation to posterior margin 10

10(9). Angle of divergence of St. IX with prominent nob at angle; 1 or 2 thick bristles (Fig. 38) .... *walkeri*
Angle of divergence without nob; 2 thick bristles (Fig. 39) .... *martini*

11(1). Finger with 2 distal spiniforms (Fig. 26) .... *durangoensis*
Finger with 3 distal spiniforms (Fig. 27) 12

12(11). Finger with oblique row of spiniforms (Fig. 13) ...... *falsicalifornicus falsicalifornicus*
Finger with vertical row of spiniforms (Fig. 27) 13

13(12). Process of clasper with long bristle (Fig. 27) 14
Process of clasper without long bristle (Fig. 26) .... *novomexicanensis*

14(13). Apex of finger distinctly acuminate (Fig. 28); posterior margin of St. IX with 1 thin, submarginal bristle .... *traubi*
Apex of finger rounded (Fig. 29); posterior margin with large number of evenly spaced bristles extending from heavy apical bristles, about ¾ down the distal arm of St. IX .... *oaxacae*

Anomiopsyllus nidiophilus
Tipton and Mendez

Figs. 7, 32, 51, 67, 78, 95

Anomiopsyllus nidiophilus Tipton and Mendez, 1968, Pacific Insects 10(1): 179.182; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus nidiophilus, though similar to *A. martini*, is the only species in the genus with one distal and three proximal spiniforms on the movable process of the clasper. Sternum VIII differs from that of all other species, except *A. sinuatus*, by having a sinus in the caudodorsal margin. The distal arm of sternum IX has a subapical constriction bearing three short, thick setae.

Female characters are not sufficiently distinctive to separate *nidiophilus* from *martini*.

Type locality: Cerro Potosi, Nuevo Leon, Mexico, 3350 m.

Type host: Nest of wood rat (probably *Neotoma albigula leucodon*).

Type specimens: Male holotype and female allotype, 38 male and 156 female paratypes, same data; 6 males and 6 females from *Neotoma albigula leucodon*, same locality as above but with dates and elevations as follows: 5 males and 2 females on 21 April 1964, 3450 m; 1 male and 2 females on 23 April 1964, 3030 m; 1 female on 11 September 1964, 3140 m; 1 female on 23 September 1964, 2990 m. Holotype and allotype in U.S. National Museum; paratypes in British Museum (Natur. Hist.), Canadian National Collection, Rocky Mountain Laboratory at Hamilton, Montana; Escuela Nacional de Cienias Biologicas (I.P.N.), Mexico, D. F.; Brigham Young University, Provo, Utah; Gorgas Memorial Laboratory, Panama; Bishop Museum and collections of R. Traub and V. J. Tipton.

Discussion: The distribution of *Neotoma albigula leucodon* is limited to the states of Coahuila, Jalisco, Mexico, Nuevo Leon, San Luis Potosi, Tamaulipas, and Zacatecas, but subspecies of *Neotoma albigula* occur in west Texas, New Mexico, Arizona, and several states in Mexico and extend northward into the southernmost areas of Colorado and Utah. Further collections are needed to define more clearly the distribution of this species in Mexico and possibly the southwestern U.S.

Anomiopsyllus amphibolus Wagner

Figs. 1-6, 30, 52, 80, 95

Anomiopsyllus nudatus Stanford, 1931 (nec Baker, 1898), Proc. Utah Acad. Sci. 8: 153 (*fide* Jellison and Good (1942: 21))

Anomiopsyllus amphibolus Wagner, 1936, Zeit für Parasitol. 8: 654-655; Jellison and Good, 1942, Index to the literature of Siphonaptera of North America: 21-24; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 114; Stanford, 1943, Proc. Utah Acad. Sci., Arts, and Lett. 19-20: 173; Costa Lima and Hathaway, 1946, Monogr. Inst. Oswaldo Cruz 4: 127; Hubbard, 1947, Bull. S. Calif. Acad. Sci. 48(3): 116; Tipton, 1950, Great Basin Nat. 10: 63; Beck et al., 1953, Proc. Utah Acad. Sci., Arts, and Lett. 30: 50; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Howell, 1957, J. Parasitol. 43(5): 40, 42; Parker and Howell, 1959, J. Parasitol. 45(6): 507-604. Stark, 1959, Siphonaptera of Utah: 105-106; Holland, 1965, Canadian Ent. 97: 1053; Beck and Allred, 1966, Brigham Young Univ. Sci. Bull., Biol. Ser. 7(2): 13; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Allred, 1968, Great Basin Nat. 28(2): 75; Tipton and Saunders, 1971, Brigham Young Univ. Sci. Bull., Biol. Ser. 15(2): 18; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsylla amphibolus (sic): Howell, 1955, Great Basin Nat. 15: 40, 42; Augustson and Durham, 1961, Bull. S. Calif. Acad. Sci. 60(2): 100.

Diagnosis: Anomiopsyllus amphibolus males may be distinguished from other *Anomiopsyllus* species, except *A. montanus* and *A. sinuatus*, by having only two widely spaced spiniforms near the posterior margin of the movable process and a single row of four very strong, heavy setae on the apical posterior margin of sternum IX, and from *A. montanus* and *A. sinuatus* by the triangular-shaped movable process. The articulation of the movable process is linear and less heavily sclerotized than in *A. nudatus*. The proximal arm of sternum IX is narrower than in *nudatus* and not parallel sided, but somewhat boomerang-shaped with the hook pointed dorsad and anterad. The distal arm of sternum IX is broad basad and gradually narrows to the apex. It is more than twice as broad at the base than at the apex, with a row of 4 heavy setae followed by 6 or 7 small setae extending ventrad two-thirds of the distance up the posterior margin from the apex. The aedeagus has a distinct mid-dorsal lobe extending from a point above the aedeagal struts one-half of the distance to the apex of the endchamber.

Females are easily distinguished from other species of *Anomiopsyllus*, except *A. montanus* and *sinuatus*, by a deep sinus of sternum VII and the straight posterior margin of tergum VIII. *Anomiopsyllus amphibolus* is distinguished from *A. montanus* and *A. sinuatus* by the presence of a bulbular expansion of the terminal portion of the blind ductus seminalis (Figs. 2, 66).

Length (average): 1.2-1.8 mm.

Type locality: Salina, Sevier County, Utah.

Type host: Neotoma desertorum

Type specimens: Male holotype and female allotype, male and female paratypes collected on 21 March 1929 by J. S. Stanford, deposited in Dr. Stanford's collection at Utah State Univ., Logan, Utah.

Recorded distribution: Nevada: Beatty, Nye Co., (Hubbard, 1949); Utah: many records (Howell, Stark).

New distribution: Arizona: Mojave and Coconino counties (north of the Colorado River); Nevada: Clark and Lincoln counties.

Material examined: Arizona: Coconino Co.: 1 female, ex *Neotoma albigula*, 3 km E of Williams (juniper woodland), 20 April 1949 (PHS); 2 males, ex *Neotoma lepida*, 55-65 km N of Williams, 2134 m (cedar), 22 April 1939 (PHS). Mojave Co.: 1 male, 1 female, ex *Neotoma lepida*, 19 km NW of Hackberry, 11 m, 8 April 1939, (PHS); 1 female, ex *Neotoma lepida*, Cutler Pockets, 10 March 1957, F. E. Durham (HF); 1 male, ex *Neotoma lepida*, Mt. Trumbull, 12 March, 1957, F. E. Durham (HF); 1 female, same host, Fulton Springs, 2 April 1959, F. E. Durham (HF); 1 female, ex *Neotoma fuscipes*[5], no specific locality, 26 April 1938 (PHS). *Nevada:* Clark Co.; 1 male, 1 female, ex *Neotoma mexicana*, 16 km N, 18 km W of Las Vegas, 2592 m, 19 March 1949; 1 female, ex *Neotoma fuscipes*, no specific locality, 14 April 1938 (PHS). Lincoln Co.: 1 female, ex *Onychomys leucogas-*

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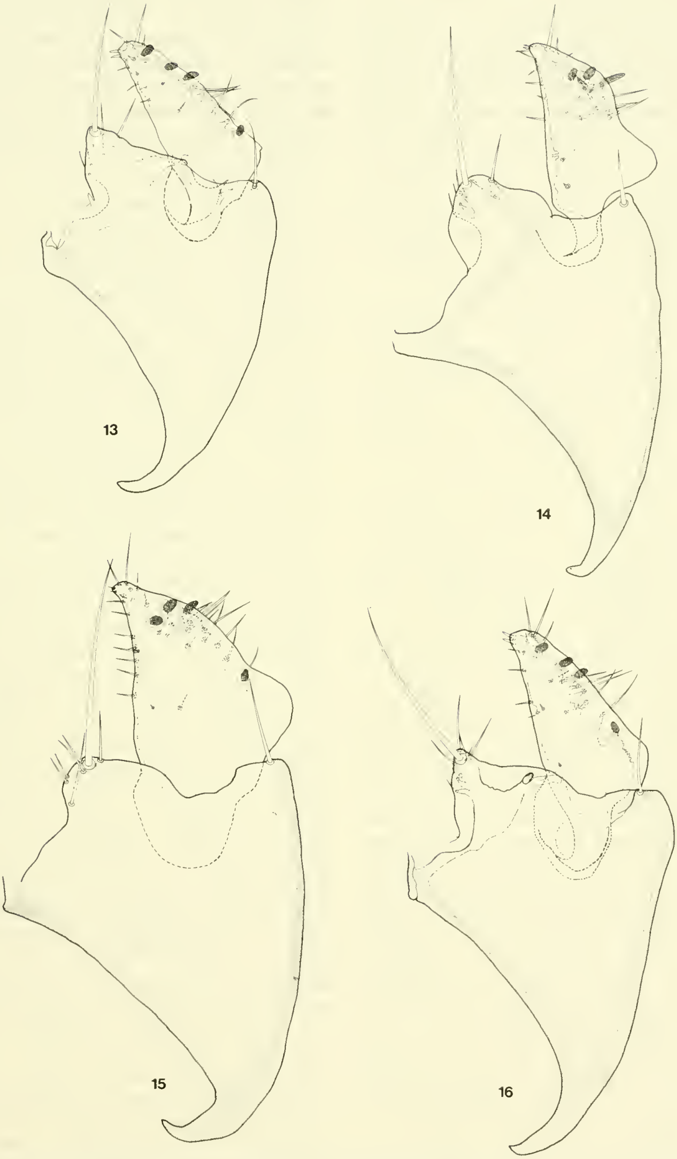
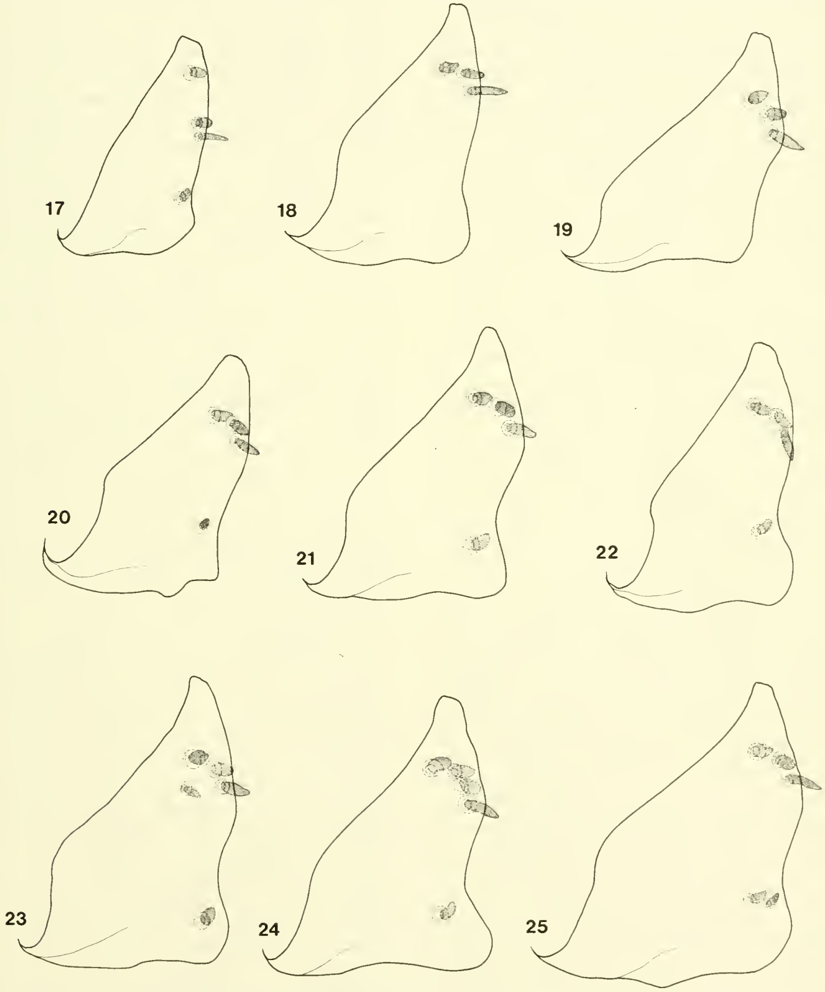
[5] The record from *Neotoma fuscipes* is undoubtedly an error, since *N. fuscipes* is not recorded from Arizona. The record should probably be ascribed to *N. albigula*.)



Figs. 13-16. Finger and clasper: 13, *A. walkeri*; 14, *A. falsicalifornicus falsicalifornicus*; 15, *A. falsicalifornicus congruens*; 16, *A. martini*.

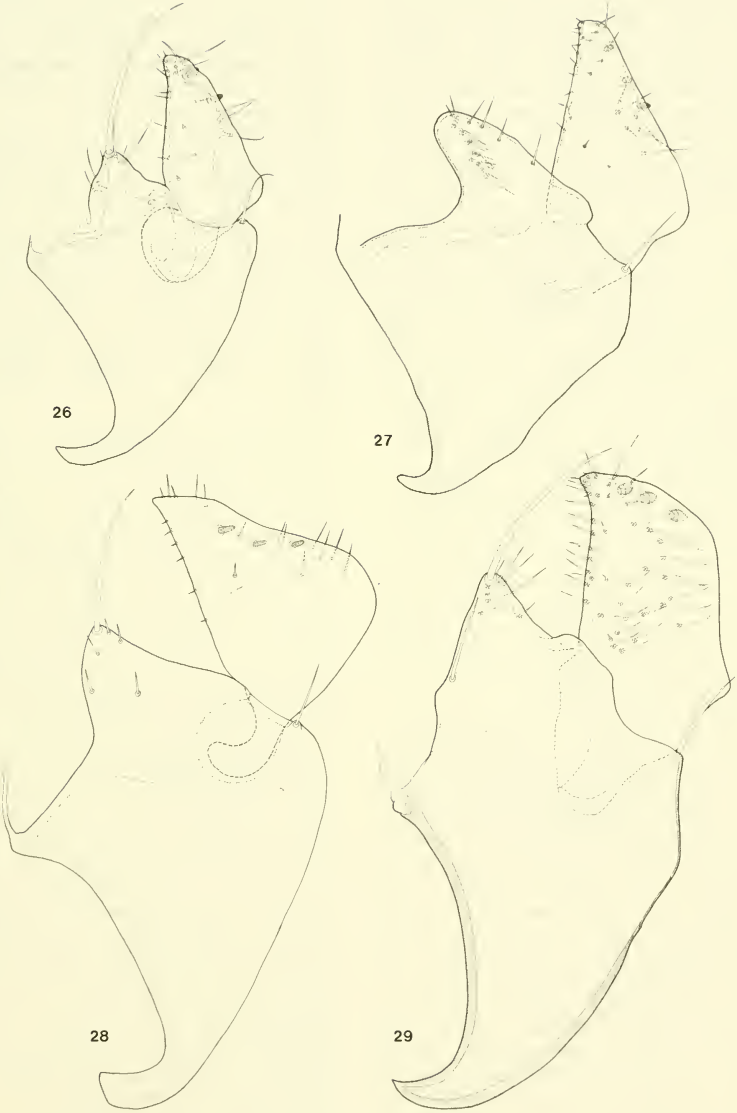
ter, 39 km SW of Caliente, 1220 m (cactus, sage), 4 May 1939 (PHS). Nye Co.: 6 males, 10 females, ex *Neotoma albigula*, 27 km NE of Pahrump, 1982 m (rocky timber), 19 December 1949, E. Kudka; 3 males, ex *Peromyscus maniculatus*, same locality, (PHS); 2 males, 4 females, ex *Neotoma lepida* nest, 28 June 1965, Merino; 1 male, ex *Neotoma lepida*, Mercury, 12 March 1961; 1 female, ex *Neotoma lepida* nest, Mercury, 15 June 1965, Merino; 1 female, same host, same location, 1 July 1965, Merino; 1 male, ex *Peromyscus*, Mercury, 6 October 1959, NAV-KAI. *Utah:* Beaver Co.: 1 female, ex *Reithrodontomys megalotis*, Wahwah Springs; 1 male, ex *Neotoma lepida*, 13-14 September 1950, D. E. Beck. Box Elder Co.: 1 male, 1 female, host not specified, Lucin small reservoir at site of abandoned CCC camp, 18 June 1952, Beck and Killpack; 2 males, 3 females, ex *Neotoma lepida*, Lucin, 14 February 1953, Beck et al. Davis Co.: 4 males, 6 females, ex *Neotoma* nest, Roy, 13 October 1951, Kohls and Sargent (RM). Duchesne Co.: 1 female, ex *Peromyscus maniculatus*, locality not stated (Bluebell, junipers), 21 March 1953, Killpack. Grand Co.: 1 male, ex *Neotoma* sp., Devil's Garden Area of Arches National Monument, 10 May 1950, D. M. Allred; 6 males, 6 females, ex *Neotoma lepida* nest, Moab S side of U 93 near willow sweeps 4.8 km W of Arches National Monument (red sandstone), 1 September 1950, D. M. Allred; 4 males, 4 females, same host, Moab 1.6 km S of US 160 and U 93 Junction (Navajo sandstone environs), 9 September 1950, D. M. Allred; 9 males, 20 females, same host, .8 km S of US 160 and U 93 Junction (Navajo sandstone environs), 9 September 1950, D. M. Allred. Iron Co.: 2 females, ex *Neotoma lepida* nest, 14.5 km W of Parowan (canyon defile), 6 September 1950, Beck and Allred. Juab Co.: 1 male, ex *Neotoma lepida*, 1.6 km NW of Joy, 1 June 1951, Allred et al.; 4 males, 10 females, same host, Fish Springs mine shaft in foothills 4.8 km N of Harris Ranch House (rocky ledges), 15 June 1951, Beck et al.; 3 males, 8 females, ex *Neotoma Lepida* nest, Lynndyl (fallen tree, consisting of juniper twigs and bark), 17 November 1951, Barnum and Moore; 30 males, 40 females, ex *Neotoma lepida*, N of Lynndyl and E of old CCC camp, same date, Barnum and Moore; 2 males, 1 female, same host, Lynndyl (juniper tree), same date, Barnum and Moore; 40 males, 39 females, ex *Neotoma lepida* nest, N of Lynndyl and E of CCC camp, 17 November 1951, Milander and Cloward; 151 males, 169 females, same host, E of Jericho (juniper), 13 December 1952, Beck et al.; 136 males, 165 females, same host, Jericho by US 6, 13 March 1954, Howell and Beck; 35 males, 74 females, same host, Jericho E side of Hwy 50-6, 4.5 km N of train station (cedar), 11 April 1954, J. F. Howell; 23 males, 49 females, same host, same location, 8 May 1954. J. F. Howell; 1 male, 8 females, same host, N of Jericho on E side of Hwy 50-6, 9 June 1954, J. F. Howell; 2 males, 2 females, same host 4.5 km N of Jericho (juniper and sage), 8 July 1954, J. F. Howell; 1 female, same host, Jericho (juniper and sage), 21 July 1954, Howell and Beck; 2 males, same host, 4.8 km N of Jericho, 3 September 1954, J. F. Howell; 1 male, 4 females, ex *Neotoma lepida lepida* nest, 4.8 km N of Jericho on US 6, 29 September 1954, J. F. Howell; 41 males, 68 females, same host, same location, 8 October 1954, J. F. Howell; 81 males, 82 females, ex *Neotoma lepida* nest, Jericho E side of US 6, 4.5 km N of train station, 6 February 1954, Howell and Beck; 18 males, 39 females, ex *Neotoma lepida*, 4.8 km N of Jericho on E side of US 6, 29 October 1954, Howell and Jaussi; 65 males, 65 females, same host, same location, 12 November 1954, Howell; 207 males, 285 females, ex *Neotoma lepida*, same location, 2 December 1954, Howell and Nielson; 40 males, 39 females, ex *Neotoma lepida* nest, 4.8 km NE Jericho, 7 January 1954, J. F. Howell; 75 males, 69 females, same host, 4.8 km NE of Jericho on E side of US 6, 25 January 1955, J. F. Howell; 12 males, 8 females, ex *Neotoma lepida*, 4.8 km NE of Jericho, 3 March 1959, BYU. Kane Co.: 1 male, ex *Dipodomys ordii*, 16 February 1972, NAV-KAI; 24 males, 7 females, ex *Neotoma albigula*, 5 December 1971, NAV-KAI; 1 female, ex *Neotoma lepida*, Navajo Wells, 24 June 1951, BYU; 1 male, 1 female, same host, 8.8

km W of Adairville in Catstaire Canyon (rocky area), 8 September 1951, Beck and Allred; 1 female, same host, Navajo Wells SW of Corral (rocky ledges), 7 September 1951, Beck and Allred; 1 male, 1 female, same host, same location, 6 September 1951, Beck and Allred; 1 male, 1 female, same host, W entrance to Catstaire Canyon (Upper Sonoran sagebrush), 9 May 1952, M. D. Coffey; 1 male, 2 females, ex *Neotoma lepida* nest, Catstaire Canyon (sagebrush), 8 May 1952, M. D. Coffey; 1 male, same host, W entrance to Catstaire Canyon (rocky ledge), same date, M. D. Coffey; 8



Figs. 17-25. Variations in spiniform placement on finger: 17, A. *nudatus mexicanus*; 18-25, A. *falsicalifornicus congruens*.

males, 9 females, ex *Peromyscus crinitus*, 11 December 1971, NAV-KAI; 1 male, 2 females, ex *Peromyscus maniculatus*, 40.2 km E of Kanab about 457 m off road near Paria and King manganese mine roads junction, 9 May 1952, M. D. Coffey; 1 male, 1 female, ex. *Peromyscus truei*, 17 February 1972, NAV-KAI. 4 males, 2 females, ex *Neotoma cinerea*, 6.4 km N of Kanab, 1494 m, 14 April 1949 (PHS). Millard Co.: 11 males, 31 females, ex *Neotoma lepida*, Lynndyl, 17 November 1951, Melander and Cloward. San Juan Co.: 1 female, ex *Neotoma albigula*, Montezuma Creek 4.8 km N of trading post, Beck et al.; 1 male, 6 females, ex *Neotoma mexicana*, Blanding, 7 September 1956; 1 male, 1 female, ex *Peromyscus maniculatus* 32.2 km S of Moab (sandy wash cliff), 7 May 1951, Allred et al.; 3 males, 2 females, ex *Neotoma lepida*, Yuba Dam 1.6 km from Hwy 28, 182.8 m W on N side of reservoir, 18 April 1952, Beck and Beck; 9 males, 9 females, ex *Neotoma lepida* nest, Yuba Dam, 29 April 1960, Beck. Sanpete Co.: 2 males, 2 females, ex *Neotoma lepida*, Yuba Dam, 18 April 1952, D. E. Beck. Tooele Co.: 1 female, ex *Neotoma lepida* 3.2 km N Little Granite Mt., 10 March 1955, E. A. Shippee (U of U); 1 male, 1 female, ex *Neotoma* sp. nest, Sandy Pars, Dugway Valley, 15 April 1954, D. Allred (U of U); 3 males, 1 female, ex *Neotoma lepida* nest, Dugway Proving Grounds, 3 March 1955 (U of U); 10 males, 7 females, same host, same location, 14 April 1955 (U of U); 1 male, 1 female, same host, same location, 6 April 1955 (U of U); 17 females, same host, same location, 6 January 1955 (U of U); 13 males, 12 females, same host, same location, 7 February 1955 (U of U); 1 male, 1 female, same host, same location, 20 January 1955 (U of U); 10 males, 12 females, same host, same location, 20 January 1955 (U of U); 10 males, 12 females, same host, same location, 16 March 1955 (U of U); 3 males, 2 females, same host, same location, 9 December 1954 (U of U); 6 females, same host, same location, 27 October 1954 (U of U); 6 males, 1 female, same host, same location, 24 November 1954 (U of U); 1 female, ex *Peromyscus truei*, Cane Springs, Cedar Mts., Dugway Proving Grounds, 21 January 1953 (U of U); 1 male, ex *Peromyscus crinitus*, Camel Back Mt., Dugway Proving Grounds, 30 January 1953 (U of U). Uintah Co.: 1 male, ex *Peromyscus maniculatus*, Dinosaur National Monument 1.2 km SSW of headquarters on N bank of river (sandy wash), 14 August 1951, Beck et al. Utah Co.: 8 males, 14 females, ex *Neotoma*, Chimney Rock Pass, 25 October 1968, Clark; 1 female, ex *Neotoma* nest, Provo, top of ladder in Buckley's mine in Rock Canyon, 24 November 1948, D. M. Allred; 1 female, ex *Neotoma cinerea*, Springville, 29 November 1948, V. J. Tipton; 2 males, ex *Neotoma cinerea* nest, Thistle (tunnel composed of rags, sticks, paper, plants, rope, and many bones), 2 November 1951, Barnum et al.; 10 males, 16 females, same host, Spanish Fork Canyon, 2 November 1951, Barnum et al.; 3 males, 1 female, same host, Spanish Fork Canyon, cave N of Ma's and Pa's Cafe in Canyon, 5 November 1951, Barnum et al.; 1 female, 2 males, ex *Neotoma lepida*, Eureka, 17 November 1951, Barnum and Moore (BYU); 1 female, ex *Neotoma cinerea*, Spanish Fork Canyon, small cave (dried plants), 2 November 1951, W. Milander; 1 female, ex *Neotoma lepida*, Elberta, Chimney Rock Pass, 15 October 1949, D. M. Allred; 19 males, 29 females, ex *Neotoma lepida* nest, Cedar Valley (juniper-rocky hillside), 22 February 1953, Beck and Coffey; 1 female, ex *Neotoma lepida*, nest, NE Chimney Rock Pass near abandoned mine, 28 March 1953, Coffey and Liddiard; 1 female, ex *Peromyscus maniculatus*, Cedar Valley on hill NE of big juniper grove, 25 March 1951, Allred et al.; 1 male, 2 females, same host, 3.2 km W of Genola on main Hwy to Eureka (rocky cliffs), 13 January 1952, D.E. Beck. Washington Co.: 1 female, ex *Neotoma lepida*, Beaver Dam Mtns., 22 April 1953, Howell; 1 male, ex *Dipodomys merriami*, W side Beaver Dam Wash bottom (alfalfa fields of Terry Ranch), 21 December 1950, Beck and Allred; 1 female, ex *Dipodomys merriami*, 3.2 km S of Rockville, 13 July 1953, Beck and Killpack; 1 female, ex *Neotoma lepida*, St. George, 25 November 1949, Allred and Barnum; 43 males, 63 females, ex *Neotoma lepida* nest, Beaver Dam Wash, .8 km NE



Figs. 26-29. Finger and clasper: 26, *A. durangoensis*; 27, *A. novomexicanensis*; 28, *A. traubi* (redrawn fom Barrera 1951 and Barnes 1963); 29, *A. oaxacae*.

Terry Ranch (joshua tree peat), 21 December 1950, Beck and Allred; 2 males, 5 females, same host, Beaver Dam Wash of Beaver Mtns. (joshua tree foothills), 23 February 1952, D. E. Beck; 1 female, ex *Neotoma lepida*, Beaver Dam Wash (flat, gravel), 16 April 1952, Grant et al.; 1 female, ex *Peromyscus eremicus*, S of Hwy 15 and Berry Springs (sandy area), 19 December 1950, Beck and Allred; 1 female, same host, Berry Springs (lava rock), 19 December 1950, Beck and Allred; 1 female, ex *Peromyscus maniculatus*, 6.4 km W of Hwy 59 state line crossing at Utah-Arizona border, 12 July 1952, Beck and Killpack; 4 females, ex *Neotoma lepida* nest, Rush Valley (juniper), 9 November 1951, Barnum et al.; 2 females, ex *Neotoma lepida* nest, Toquerville, 5 September 1951, Beck and Allred. *Wyoming:* Sweetwater Co.: 1 female, ex *Neotoma cinerea*, 24 km SW of Green River, 1920 m (rocky ledges), 23 August 1938 (PHS).

Discussion: This species is most closely related to *A. montanus*. Characteristics of the male clasper, e.g., configuration of the fixed process of the clasper and presence of a row of setae above the acetabular seta (Fig. 6), show relationship between males of these two species. The shape of the spermatheca and configuration of sternum VII (Fig. 80) indicate a relationship between the females of these two species.

With the exception of *A. montanus*, *amphibolus* occurs farther north than any other species of *Anomiopsyllus*, and it is the Great Basin representative of the genus. The distributional pattern includes northwestern Arizona from whence it extends northward between the Rocky Mountains and the Sierra Nevada Mountains into Wyoming. The species has been recorded most frequently from Utah where much research has been conducted by Allred, Beck, Howell, and Tipton at Brigham Young University and Stanford at Utah State University. This species has also been recorded from Nye and Douglas counties, Nevada (Beck et al. 1953, Hopkins and Rothschild 1962). Its distribution may include those parts of eastern and northeastern California which have a habitat similar to that of the Great Basin and where *Neotoma lepida* occurs, but we have not collected *A. amphibolus* from that area during this study.

The primary host appears to be *Neotoma lepida*, although records include *N. cinerea* and *Peromyscus* in frequent numbers. Records from fortuitous hosts are most often obtained during plague surveys.

Stark (1959) has pointed out that *A. amphibolus* may prefer dry habits, since nests of *N. cinerea* occurring at high elevations (noted in Beck et al. 1953) had fewer fleas per nest than those of *N. lepida* occurring at lower elevations. This fails to take into consideration possible host differences, which may be a significant factor. *Neotoma cinerea* has been placed in a separate subgenus by Goldman (1910), Hall and Kelson (1959), and others, and may well differ significantly from the standpoint of flea host selection.

Howell (1957) states that in the vicinity of Jericho, Juab County, Utah, *A. amphibolus* adults appear in nests of *N. lepida* in October and reach a peak in December. This seasonal distribution almost duplicates that of *A. falsicalifornicus* in California.

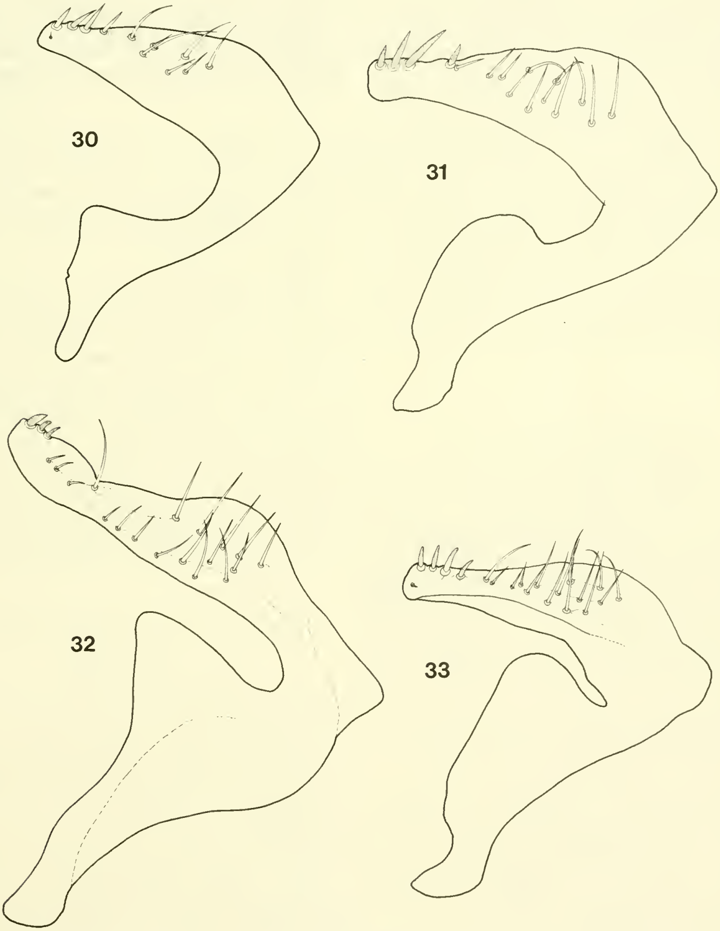
Among the many specimens examined, very little variation was evident; *A. amphibolus* from northwestern Arizona did not differ in any significant detail from specimens collected in Utah. This is in distinct contrast to some *Anomiopsyllus* species, e.g. *A. falsicalifornicus*, which shows considerable variation both geographically and among individuals in a series. The apparent stability of *A. amphibolus* over a broad area may be explained in part by the rather continuous distribution of its host, *N. lepida*, through the Great Basin (see Hall 1946). The climate of the Great Basin, though complex, changes primarily with latitude and altitude. Populations of *A. amphibolus* would be expected to be relatively continuous with much opportunity for uninterrupted gene flow. The area occupied by *A. falsicalifornicus* is subject to more climatic variability resulting not only from very heterogeneous topography and latitude, but also from proximity to or distance from the sea. Populations of *A. falsicalifornicus* are disjunct in their distribution (of both the total population and especially the local populations) which results in much gene flow interruption.

Anomiopsyllus sinuatus Holland

Figs. 9, 33, 54, 65, 79, 94

Anomiopsyllus sinuatus Holland, 1965, Canadian Ent. 97: 1053, 1058; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus sinuatus is closely related to *A. montanus* in that both have the movable process L-shaped with a large, blunt spiniform mesally inserted at the distal and proximal portions. *Anomiopsyllus sinuatus* has a broader, shorter process than *montanus*. The ninth sternum differs from that of *A. montanus* by the presence of three thickened setae followed by a row of thinner setae as compared to four thick setae in *A. montanus*. The sinus formed by the inner margins of the proximal and distal arms is deep and narrow in



Figs. 30-33. Male ninth sternum: 30, *A. amphibolus*; 31, *A. montanus*; 32, *A. nidiophilus*; 33, *A. sinuatus*.

sinuatus and broadly rounded in *montanus*. *Anomiopsyllus sinuatus*, like *A. montanus*, has a sinus on the caudal border of sternum VIII.

Female characters are not sufficiently distinctive to separate *sinuatus* from *montanus*.

Type locality: 48 km W of Durango, Durango, Mexico, 1982 m.

Type host: Nest of *Peromyscus* sp.

Type specimens: Male holotype and female allotype, 4 male and 11 female paratypes collected on 5 June 1961 by J. E. H. Martin, deposited in the Canadian National Collection.

Discussion: Anomiopsyllus sinuatus and *A. montanus* present an interesting distributional problem in that *montanus* has only been collected at the northern distribution of *Anomiopsyllus* and *sinuatus* has only been collected at the southern portion. Collections so far have not indicated that there are any intermediate forms between these two populations; however, further specimens should be collected with the view of linking these geographically separated species.

Anomiopsyllus montanus Collins

Figs. 8, 31, 53, 66, 81, 94

Anomiopsyllus montanus Collins, 1936, Ent. News 47: 128-130; Ewing and I. Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 115; Hubbard, 1947, Fleas of western North America: 82-83; Holland, 1952, Canadian Ent. 84(3): 65-72; Holland, 1965, Canadian Ent. 97: 1053, 1055, 1058; Senger, 1966, J. Kans. Ent. Soc. 39(1): 106; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Jellison and Senger, 1973, Mont. Agr. Exp. Sta. Res. Rept. 29: 18-19; Lewis 1974, J. Med. Ent. 11(2): 154.

Arctopsylla montanus: Jellison, Kohls, and Mills, 1943, Mont. State Board Ent. 2: 2 (error for *Anomiopsyllus*).

Anomiopsyllus nudatus: Dunn and Parker, 1923, Public Hlth. Rept. 38: 2774-2775 (misidentification).

Diagnosis: Anomiopsyllus montanus is closely related to *A. sinuatus* but differs in that there are four heavy setae near the apex of sternum IX instead of three as in *sinuatus*. The movable process of *A. montanus* is narrower and longer with a deeper sinus than in *sinuatus*.

Female characters are not sufficiently distinctive to separate *montanus* from *sinuatus*.

Type locality: Canyon Creek, W of Hamilton, Montana.

Type host: Bubo virginianus occidentalis

Type specimens: Male holotype and female allotype collected in 1922 by L. H. Dunn and R. R. Parker, deposited in the National Institutes of Health.

Discussion: This flea was first collected from a horned owl (*Bubo virginianus*) near Hamilton, Montana, and identified as *Anomiopsyllus nudatus* by Dunn and Parker (1923). Collins (1936) rectified the misdetermination and described the species as new.

Subsequent records have been few. We have examined only material from near Hamilton, Montana, from *Bubo virginianus* (part of the original series) and *Neotoma cinerea*. Holland (1952) recorded the species from near Banff, Alberta, Canada. No other records are available.

Anomiopsyllus montanus has the northernmost distribution of any species in the genus. We suspect that the primary host is a species of *Neotoma*, possibly *N. cinerea* since no other *Neotoma* species occurs as far north as Hamilton, Montana, and Alberta, Canada (Hall and Kelson 1959). The original discovery of this flea on the horned owl should not be considered too unusual, as fleas are often found on the predators of their hosts. In addition, horned owls often nest in cliffs, which are a preferred nesting site of *N. cinerea*.

Anomiopsyllus nudatus nudatus (Baker)

Figs. 11, 36, 55, 68, 84, 94

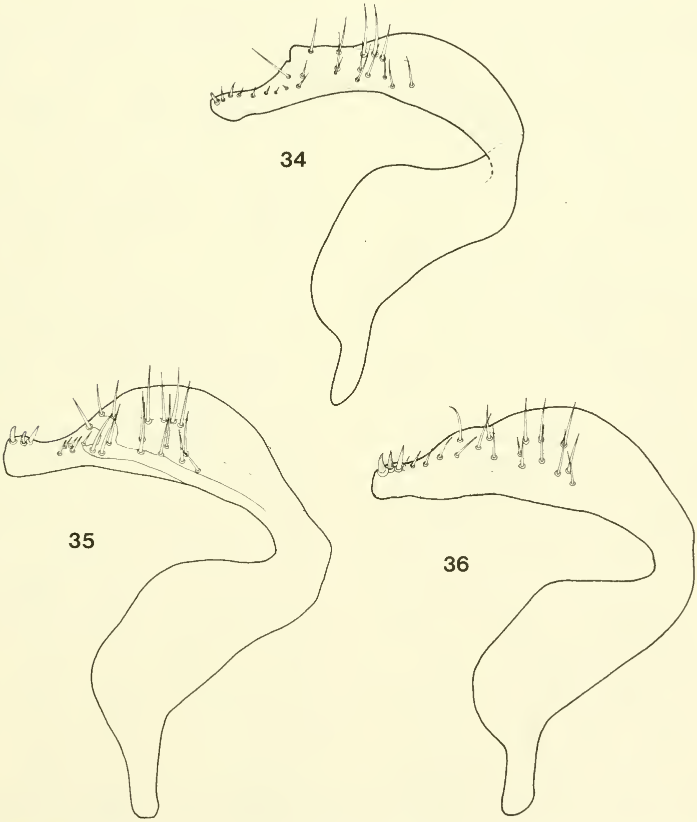
Typhlopsylla nudata Baker, 1898, J. N. Y. Ent. Soc. 6: 56.

Anomiopsyllus nudatus Baker, 1904, Proc. U.S. Nat. Mus. 27: 425, 426, 452; Fox, 1914, Hyg. Lab. Bull. 97: 25; Jordan and Rothschild, 1915, Ectoparasites 1: 45; Dunn and Parker, 1923, Public Hlth. Repts. 38: 2774-2775; Fox, 1929, Ent. News 40: 218; Hirst, 1926, Ceylon J. Sci. 1: 261; Wagner, 1930, Mag. de Parasitol. 1: 135; Stanford, 1931, Proc. Utah Acad. Sci. 1931: 153; Collins, 1936, Ent. News 47: 129-130; Eskey and Haas, 1939, Public Hlth. Repts. 54: 1472; Eskey and Haas, 1940, Public Hlth. Bull. 254: 29-74; Hubbard, 1940, Pac. Univ. Bull. 37(4); Augustson, 1943, Bull. South. Calif. Acad. Sci. 42(2): 73; Ewing and I.

Fox, 1943, U.S. Dept. Agric. Misc. Publ. 500: 115; Hubbard, 1947, Fleas of western North America: 79-80; Eads and Menzies, 1948, J. Kans. Ent. Soc. 21: 135; Hubbard, 1949, Bull. South. Calif. Acad. Sci. 48: 125; Pollitzer, 1952, Bull. WHO 7: 231-342, Annex 1; Augustson and Wood, 1953, Bull. South. Calif. Acad. Sci. 52: 48-56; Wehrle, 1953, Pan-Pacific Ent. 24: 39; Holdenreid and Morlan, 1955, J. Inf. Dis. 96: 135; Augustson, 1955, Bull. South. Calif. Acad. Sci. 54(1): 36-39; Knudsen, 1956, Bull. South. Calif. Acad. Sci., 55(1): 1-63; Beer et al., 1959, J. Parasitol. 45(6): 605-623; Stark, 1959, Siphonaptera of Utah: 107; Holland, 1965, Canadian Ent. 97: 1051-1058; Barnes, 1965, Pan-Pacific Ent. 41(4): 272-280; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Tipton and Saunders, 1971; Brigham Young Univ. Sci. Bull., Biol. Ser. 15(2): 18; Pratt and Stark, 1973, DHEW Publ. 74-8267: 11; Haas et al., 1973, J. Med. Ent. 10(3): 282; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsyllus californicus: Baker, 1904, Invert. Pac. 1: 39-40; Fox, 1926, Pan-Pacific Ent. 2: 183-184.

Diagnosis: The three subspecies of *A. nudatus: nudatus, mexicanus,* and *hiemalis* can only be distinguished from each other by characters in the males. This separation is based on characters of the movable process and sternum IX. *Anomiopsyllus nudatus nudatus* can be separated readily from the other two subspecies by the presence of two closely spaced (less than 20 u) spiniforms on the distal portion of the movable process and the presence of a thin bristle at the arc



Figs. 34-36. Male ninth sternum: 34, *A. nudatus hiemalis*; 35, *A. nudatus mexicanus*; 36, *A. nudatus nudatus.*

of curvature of the distal arm of sternum IX. The movable process of the clasper in *nudatus nudatus* is narrow (M = 68 u, range 58 to 74 u) at base measured at the widest point and relatively short (M = 109 u, range 102 to 119 u).

Female characters are not sufficiently distinctive to separate the subspecies of *nudatus.*

Length: (average)—Male, 1.2 mm; female, 1.8 mm.

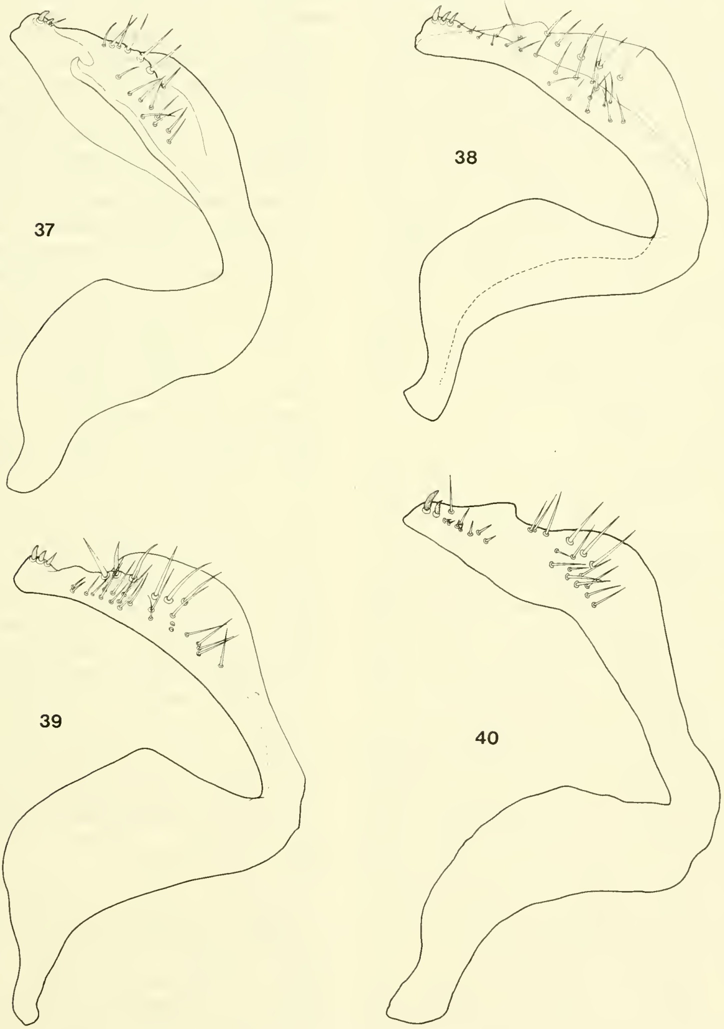
Type locality: Tucson, Pima Co., Arizona.

Type host: Neotoma albigula.

Type specimen: Female, U.S. National Museum.

Material examined: Arizona: Cochise Co.: 1 male, ex *Neotoma lepida*, 29 October 1938 (PHS); 1 male, ex *Neotoma lepida*, no date (PHS). Pima Co.: 1 female, ex *Neotoma lepida*, 7 February 1939 (PHS); 1 female, ex *Neotoma lepida*, 3 November 1938 (PHS); 1 female, ex *Neotoma lepida*, 4 November 1938 (PHS); 1 female, ex *Dipodomys merriami*, 7 February, 1939 (PHS); 1 male, ex *Spermophilus harrissi*, 8 February 1939 (PHS). *California:* Kern Co.: 1 male, ex *Neotoma* sp. Burbank Girl Scout Camp, Frazier Mtn. (oak, pine), 2 June 1958, Campbell (BVC); 1 female, ex *Neotoma fuscipes* nest, 0.8 km E of Frazier Park (oak woodland), 1 April 1959, Barnes (BVC); 17 males, 37 females, ex *Neotoma fuscipes* nests, 6.9 km N, 3.7 km W of Willow Springs (juniper woodland), 19 February 1959; 25 males, 54 females, same host, same locality, 22 January 1960. Los Angeles Co.: 13 males, 34 females, ex *Neotoma fuscipes* nests, 7.7 km N, 3 km W of Sandburg (oak woodland), 1 April 1959, Barnes (BVC); 10 males, 28 females, ex *Neotoma fuscipes* nests, 4.5 km S, 1477 km W of Fairmount (juniper woodland), 1 April 1959, Barnes (BVC); 8 males, 17 females, ex *Neotoma fuscipes*, 2.2 km S of Gorman (oak, yucca), 1 April 1959, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, School Canyon 5.9 km E of Glendale (oak woodland), 28 January 1959, D. Rohe (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, Burbank (oak woodland), 6 April 1959, D. Rohe (BVC); 3 males, 2 females, ex *Neotoma lepida*, Big Tujunga Canyon, 4 January 1942, J. Couffer (HF); 1 male, 3 females, ex *Neotoma lepida*, San Gabriel Canyon, 15 January 1942, G. Augustson (HF); 3 males, 1 female, ex *Neotoma* nest, Chilao, 16 August 1942, G. Augustson (HF). Orange Co.: 1 female, ex *Neotoma* sp., Irvine (cactus, *Nicotiana*), 19 April 1955, J. Poll (BVC); 1 male, 1 female, ex *Neotoma* sp., same locality (cactus, *Nicotiana*), 26 March 1957, E. Perry (BVC); 5 males, 6 females, ex *Neotoma* sp., same locality (cactus, *Nicotiana*), 19 November 1952, J. Poll (BVC); 12 males, 20 females, ex *Neotoma fuscipes* nest, Santiago Canyon (cactus, *Nicotiana*), no date, G. Augustson (HF). Riverside Co.: hundreds, ex *Neotoma fuscipes*, San Timoteo, many dates, R. Ryckman; 3 females, ex *Neotoma* sp., 1.6 km E of McAfee Ranch, San Timoteo Canyon, 18 March 1955, J. Poll (BVC); 6 females, ex *Neotoma* nest, Matthew Lake, 3 February 1951, Ames; 4 females, ex *Neotoma lepida*, Matthew Lake, 3 February 1951, Ames; 2 males, 9 females, ex *Neotoma lepida*, Matthew Lake, 8 February 1951, Ames. San Bernardino Co.: 2 males, 1 female, ex *Neotoma lepida*, San Bernardino (oak woodland and chaparral), 21 March 1957, Barnes (BVC); 1 female, ex *Neotoma lepida*, 5.4 km N, 6.4 km E of Pioneer Town (joshua tree, yucca), 3 December 1956, K. Murray (BVC); 8 males, 3 females, ex *Neotoma lepida*, 3.2 km to 3.8 km NW of Yucca Valley (yucca desert), 4 December 1956, K. Murray (BVC); 68 males, 144 females, ex *Neotoma fuscipes* nest, 1.6 km E of Cajon (heavy chaparral), 22 December 1957, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes* nest, 3.5 km SE of Desert Springs (juniper woodland), 22 January 1959, Barnes (BVC); 1 female, ex *Neotoma* sp., George Air Force Base, Victorville (juniper woodland), 25 October 1951, J. Poll (BVC); 1 male, 2 females, ex *Neotoma* sp., Big Bear Lake (oak, pine), 30 May 1951, J. Poll (BVC); 1 female, ex *Neotoma* sp., Seven Oaks, 10 May 1936 (RM); 1 male, 8 May 1936 (RM); 1 female, ex *Neotoma lepida*, Batista Canyon, 28 February 1951, Ames. San Diego Co.: 5 males, 9 females, ex *Neotoma fuscipes* nests, 3 km E of Banner (juniper, *Rhus ovata* woodland), 23 March 1960, Barnes (BVC); 10 males, 9 females, ex *Neo-*

toma fuscipes nest, 16 km E of Ramona (oak woodland), 23 March 1960, Barnes (BVC); 65 males, 122 females, ex *Neotoma fuscipes* nest, Alvarado Canyon, San Diego (oak wood and chaparral), 21 March 1960, Barnes (BVC); 1 male, ex *Neotoma fuscipes* nest, 7 km S of Julian, 1219 m (oak woodland), 22 March 1960, Barnes (BVC); 4 males, 1 female, ex *Neotoma* nest, 3 km W of Guatay (oak woodland), 2 September



Figs. 37-40. Male ninth sternum: 37, *A. falsicalifornicus falsicalifornicus*; 38, *A. walkeri*; 39, *A. martini*; 40, *A. falsicalifornicus congruens.*

1955, H. Stark (PHS); 1 female, ex *Neotoma* sp., San Diego, 1936, Eskey (PHS). Ventura Co.: 2 males, 7 females, ex *Neotoma fuscipes* nests, Alder Creek 987 km N, 2.9 km W Fillmore, 28 January 1960, Barnes (BVC); 1 male, 1 female, ex *Neotoma* sp., Ozena Public Camp 2.5 km E of Hwy. 399, 26 March 1957, J. Poll (BVC); 1 male, ex *Neotoma* sp., Sycamore Canyon, 29 June 1955, E. Perry (BVC). *Nevada:* Nye Co.: 1 male, ex *Neotoma lepida*, Beatty, no date. *Utah:* San Juan Co.: 1 male, ex *Peromyscus maniculatus*, 32 km S of Moab, 8 May 1951, (Tipton and Allred); 1 male, 2 females, ex *Neotoma albigula*, Recapture Canyon, 1738 m, 16 August 1939 (PHS); 1 male, 1 female, ex *Neotoma mexicana*, Westwater Canyon, 3.2 km S of Blanding, 1830 m, 19 August 1939 (PHS).

New distribution: Arizona: Cochise Co. (PHS); *California:* Kern Co. (BVC), Riverside Co. (BVC, Ryckman), San Bernardino Co. (BVC), San Diego Co. (BVC and PHS), Ventura Co. (BVC).

Discussion: C. F. Baker (1898) described *A. nudatus* on the basis of "... two females collected by Mr. Hubbard from the inner nest of *Neotoma albigula* at Tucson, Arizona," placing the species in the genus *Typhlopsylla*, pending better knowledge of its relationships. Later, Baker (1904) described the species further and created the new genus *Anomiopsyllus* to contain it and the concurrently described *A. californicus* from Claremont, Los Angeles County, California (based on a series of females).

Baker, at the time of the original description of *nudatus*, did not designate either of his two female specimens as types, but both were deposited in the U.S. National Museum. Since both specimens were collected in the Sonoran Desert at Tucson, Arizona, the subspecies occupying that area becomes the nominate subspecies. Jordan and Rothschild's male allotype, unfortunately, falls into another subspecies occupying the Colorado Plateau from eastern Arizona through New Mexico. Though their specimen was not available for study, the figure in the original description (Jordan and Rothschild 1915) is quite clearly that of the *A. n. mexicanus*. The same figure is reproduced in Hopkins and Rothschild (1962). Nevertheless, their specimen is the first described male for the genus and for the species.

Jordan and Rothschild (1915) examined Baker's types and declared *californicus* a synonym of *nudatus* on the basis of similarities in the spermathecae and in characters of the metatarsal setae. Jordan and Rothschild described and figured a male of *nudatus* from Paradise, Arizona, designating their specimen as allotype. Although their specimen is of *nudatus*, the "allotypic" locality falls within the range of *A. n. mexicanus*. Their figure of the movable process is clearly that of *mexicanus*.

Carroll Fox (1926) acquired a series of *Anomiopsyllus* from Claremont, California, the type locality of *californicus*, which included a male differing from that described as *nudatus* by Jordan and Rothschild. He, therefore, concluded the latter authors to be in error concerning the synonomy, and described the new male as allotype of Baker's revived *A. californicus*. Jordan, on examining Fox's series, found two species; one "true *californicus*" identical to Baker's types, the other a new species requiring a name (Fox 1929). Fox (1929), therefore, named the species *A. falsicalifornicus*, based on his 1926 description. Collins (1936), in separating *A. montanus* from *nudatus*, agreed with Jordan and Rothschild's synonomy and figured the female sternum VII of both *nudatus* and *falsicalifornicus*.

Neither the characters used by Baker nor those used by Jordan and Rothschild (1915) are tenable. No character involving tarsal setation or shape of spermatheca has been found reliable in this study. Nevertheless, sternum VII of females offers some degree of reliability which, together with distributional evidence, confirms Jordan and Rothschild's synonomy.

As treated here, *A. nudatus* includes three subspecies, differentiated on the basis of male morphological characters, geographic distribution, and habitat. *Anomiopsyllus hiemalis* Eads and Menzies (1948) is reduced to subspecific rank under *A. nudatus* (Baker 1898); *A. hiemalis mexicanus* (Holland 1965) is also transferred here as a subspecies of *A. nudatus*.

Phenotypic characters used to differentiate these subspecies are length and width of the movable process, distance between spiniforms of the movable process, and presence or absence of modified setae on the posterior margin of sternum IX. Measurements were made by means of a calibrated ocular grid at 430 X; the grid units were then converted to microns. Length and width measurements of the movable process were made along the longitudinal axis from the tip of the process to the "notch." The width was measured at an approximate right angle from the "notch" across the broadest part of the process. Measurements between the distal pair of spiniform setae were from center to center *at the base* of each spiniform.

Anomiopsyllus nudatus mexicanus Holland, n. comb.

Figs. 12, 35, 57, 70, 83, 94

Anomiopsyllus nudatus: Holdenreid and Morlan, 1955, J. Inf. Dis. 96: 135; Stark, 1959, Siphonaptera of Utah: 107.

Anomiopsyllus hiemalis mexicanus Holland, 1965, Canadian Ent. 97: 1056; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Males of *A. n. mexicanus* are separable from *A. n. nudatus* and *A. n. hiemalis* by the presence of a heavy bristle at the arc of curvature of sternum IX. The movable process of the clasper is longer than in *nudatus* or *hiemalis* (M = 118 u, range 100 to 133 u) and about equal to *nudatus* in width. The distance between the distal spiniform pair is greater than in *nudatus*, but less than in *hiemalis* (M = 29 u, range 23 to 35 u).

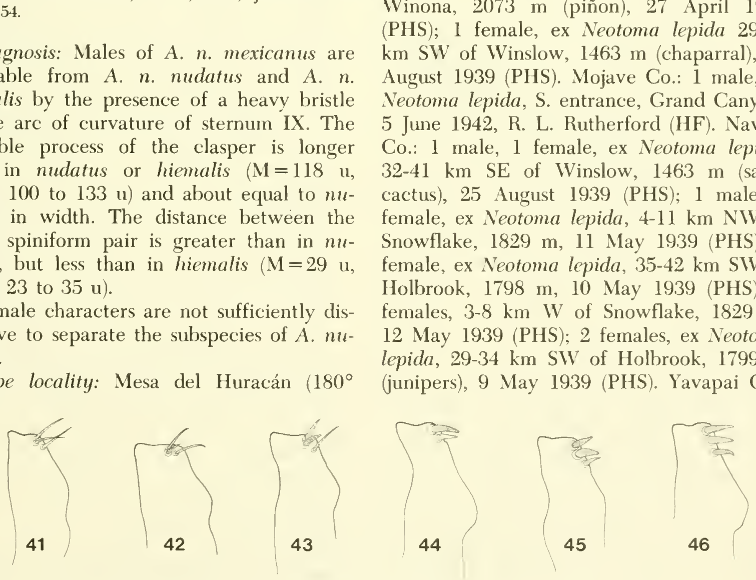
Female characters are not sufficiently distinctive to separate the subspecies of *A. nudatus.*

Type locality: Mesa del Huracán (180° 15′ W, 29° 40′ N), Chihuahua, 2256 m.

Type host: nest of *Neotoma* sp.

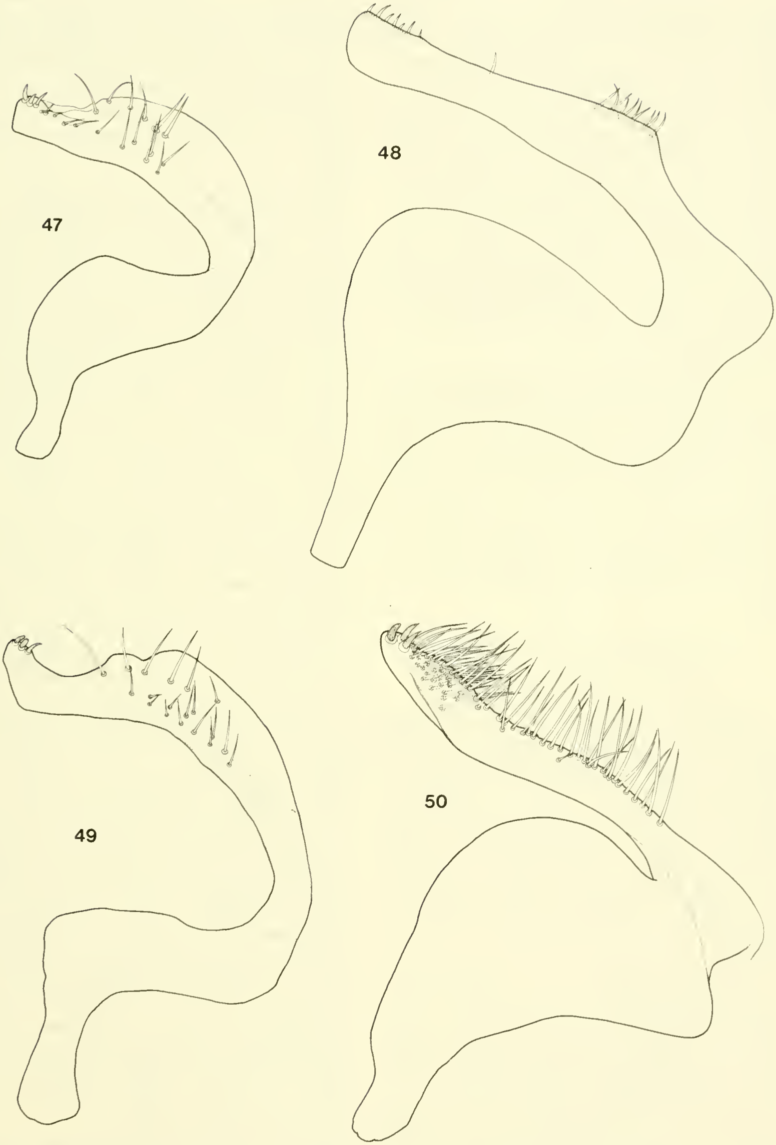
Type specimens: Male holotype and male paratype collected on 21-25 July 1964 by J. E. H. Martin, deposited in Canadian National Collection.

Material examined: Arizona: Apache Co.: 1 male, 2 females, ex *Neotoma lepida*, 44 km W of Springerville, 2302 m (cactus), 1 October 1938 (PHS); 1 male, ex *Neotoma* sp., 24 km W of Springerville, 1829 m (grass), 26 September 1938 (PHS). Coconino Co.: 1 female, ex *Neotoma albigula*, Pine Forest, 9.7 km SE of Red Lake, 2073 m (grass, cedars), 30 April 1938 (PHS); 1 male, 2 females, ex *Neotoma albigula*, 29-32 km SW of Winslow, 1463 m (chaparral), 23 August 1939 (PHS); 1 female, ex *Peromyscus maniculatus*, Pine Forest, 9.7 km SE of Red Lake, 2073 m (grass, cedars), 30 April 1938 (PHS); 1 female, ex *Peromyscus maniculatus*, 55-65 km N of Williams, 2134 m (cedar), 22 April 1938 (PHS); 1 male, ex *Neotoma lepida*, 55-60 km N of Williams, 2134 m (cedar), 22 April 1939 (PHS); 1 female, 1 male, ex *Neotoma lepida*, 3-6 km SW of Winona, 2073 m (piñon), 27 April 1939 (PHS); 1 female, ex *Neotoma lepida* 29-32 km SW of Winslow, 1463 m (chaparral), 22 August 1939 (PHS). Mojave Co.: 1 male, ex *Neotoma lepida*, S. entrance, Grand Canyon, 5 June 1942, R. L. Rutherford (HF). Navajo Co.: 1 male, 1 female, ex *Neotoma lepida*, 32-41 km SE of Winslow, 1463 m (sage, cactus), 25 August 1939 (PHS); 1 male, 1 female, ex *Neotoma lepida*, 4-11 km NW of Snowflake, 1829 m, 11 May 1939 (PHS); 1 female, ex *Neotoma lepida*, 35-42 km SW of Holbrook, 1798 m, 10 May 1939 (PHS); 3 females, 3-8 km W of Snowflake, 1829 m, 12 May 1939 (PHS); 2 females, ex *Neotoma lepida*, 29-34 km SW of Holbrook, 1799 m (junipers), 9 May 1939 (PHS). Yavapai Co.:



Figs. 41-46. Variations in apex of male ninth sternum of *A. falsicalifornicus congruens.*

4 males, 3 females, ex *Neotoma cinerea*, 22 km E of Seligman, 22 April 1938 (PHS); 1 male, ex *Neotoma cinerea*, 6 km S of Ashfork, 1585 m (rocky), 27 April 1938 (PHS); 1 male, 1 female, ex *Peromyscus* sp., 23 km E of Seligman, 1616 m, 22 April 1938 (PHS); 1 male, 1 female, ex *Peromyscus* sp., 8 km W of Seligman, 1573 m (juniper), 19 April 1938 (PHS); 3 males, ex *Peromyscus* sp., 6 km S of Ashfork 1585 m (rocky), 27 April 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida*, 16 km SW of Seligman, 1585 m, 20 April 1938 (PHS); 4 males, 3 females, ex *Neotoma lepida*, 8 km NW of Clarkdale, 1067 m, 21-22 April 1938 (PHS); 3 females, ex *Neotoma lepida*, 10 km SE of Cottonwood, 23 April 1938 (PHS); 2 females, ex *Neotoma lepida*, near Wickenburg, 19 April 1938 (PHS); 2 females, ex *Neotoma albigula*, 16 km N of Paulden, W side of Verde River, 22 April 1938 (PHS), 1 male, 1 female, ex *Neotoma albigula*, 5 km NW of Dewey, 1524 m (grass, clay), 16 April 1937 (PHS) 1 male, 1 female, ex *Neotoma lepida*, 823 m, 13 April 1938 (PHS). *Colorado*: La Plata Co.: 1 female, ex *Neotoma lepida*, Hillside 10 km N of Durango, 2012 m (oaks), 13 June 1939 (PHS). Las Animas Co.: 2 males, 1 female, ex *Neotoma* sp., 5 June 1943 (PHS); 1 female, ex *Neotoma albigula*, Las Animas, 20 June 1941 (PHS). *Kansas:* Logan Co.: 1 male, 2 females, ex *Neotoma* sp., 30 May 1945 (PHS). *Nebraska:* Morrill Co.: 3 males, 2 females, ex *Neotoma albigula*, 20 May 1949 (PHS). *New Mexico:* Bernalillo Co.: 2 females, ex *Neotoma albigula*, Cedro Canyon, 3 km SE of Tijeras, 1677 m (sage, juniper), 20 May 1939 (PHS). Catron Co.: 3 males, 3 females, ex *Neotoma albigula*, 13 km N of Alma, 1524 m (juniper), 20 May 1939 (PHS); 1 male, ex *Neotoma albigula*, 3.2 km E of Alma, 1402 m (sage), 17 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 8-16 km N of Glenwood, 1402 m, 16 May 1939 (PHS); 1 male, ex *Dipodomys ordii*, 3 km E of Alma, 1402 m (sage), 17 May 1939 (PHS); 2 males, ex *Neotoma lepida*, same locality, 17 May 1939 (PHS); 1 female, ex *Spermophilus variegatus*, between Pleasanton and Mogollon, 1829-2134 m (grass), 25 April 1939 (PHS); 1 female, ex *Peromyscus truei*, 1.6-4.8 km S of Pleasanton, 1402 m (juniper), 19 May 1939 (PHS); 1 male, 2 females, ex *Neotoma mexicana*, 10 km NE of Adams Diggings, 2287 m (prairie, junipers) 16 August 1938 (PHS); 1 female, ex *Neotoma mexicana*, Cibola Forest, 10 km W of Datil, 2439 m (juniper), 20 August 1938 (PHS); 1 female, ex *Neotoma mexicana*, 1.6 km SW of Datil, 2378 m (range, juniper), 24 August 1938 (PHS). Colfax Co.: 1 female, ex *Neotoma* sp., 4 June 1943 (PHS). Grant Co.: 2 males, ex *Peromyscus eremicus*, 3-11 km NW of Silver City, 1829 m (grass), 25 April 1939 (PHS); 1 male, 9 females, ex *Neotoma albigula*, Fort Bayard Reservation, 1829 m (grass), 28 April 1939 (PHS); 1 male, 7 females, ex *Neotoma albigula*, 3-11 km NW of Silver City, 1829 m (brush), 29 April 1939 (PHS); 6 males, ex *Neotoma albigula*, 19-22 km SE of Silver City, 1768 m (juniper), 27 April 1939 (PHS), 1 male, 1 female, ex *Neotoma albigula*, 6-8 km NW of Silver City, 1829 m (cactus), 22 April 1939 (PHS); 1 female, ex *Dipodomys merriami*, 19-22 km SE of Silver City, 1768 m (juniper), 27 April 1939 (PHS). Lincoln Co.: 2 males, 2 females, ex *Neotoma albigula*, 43 km E of Capitan, 1936 m (rocky timber), 18 April 1949 (PHS). Rio Arriba Co.: 1 male, ex *Peromyscus* sp., 5 km W of Coyote, 2591 m (timber), 10 June 1949 (PHS). San Miguel Co.: 1 male, 1 female, ex *Peromyscus* sp., Pecos, 22 February 1941, McMurray (RM). Sante Fe Co.: 14 males, 6 females, ex *Neotoma albigula* nests, Steel Ranch, November and December 1951, H. B. Morlan, 5 males, 10 females, ex *Neotoma albigula*, 23-25 May 1939 (PHS); 1 male, ex *Peromyscus maniculatus*, same locality, 23 May 1939 (PHS). Sierra Co.: 1 male, ex *Neotoma albigula*, 8-9.6 km S of Hillsboro, 1555 m (sandy), 28 June 1939 (PHS); 1 female, ex *Neotoma albigula*, Canyon, 6 km W of Hillsboro, 1677 m (cactus), 18 April 1939 (PHS); 2 males, 6 females, ex *Neotoma albigula*, Range, 3 km E of Winston, 1677 m (juniper), 21 April 1939 (PHS). Socorro Co.: 1 male, 2 females, ex *Neotoma albigula*, 4.8-8 km NW of Magdalena, 2403 m (juniper), 23 June 1939 (PHS) (type series); 1 male, ex *Neotoma albigula*, 3-6 km NW of Magdalena, 2403 m (juniper), 22 June 1939 (PHS); 1 male, 1 fe-



Figs. 47-50. Male ninth sternum: 47, *A. durangoensis*; 48, *A. traubi* (redrawn from Barrera 1951 and Barnes 1963); 49, *A. novomexicanensis*; 50, *A. oaxacae*.

male, ex *Neotoma albigula*, 16 km W, 9.6 km N of Magdalena, 2348 m, 6 May 1948 (PHS). Taos Co.: 1 female, ex *Neotoma mexicana*, 27 km S of Taos, 1829 m (sage, juniper), 17 August 1948 (PHS). Valencia Co.: 1 male, 1 female, ex *Neotoma* nest, 11 km SE of El Morro (lava outcrop), 14 June 1950 (PHS). *Utah:* Beaver Co.: 2 males, ex *Neotoma* sp., 8 May 1945 (PHS); 1 female, ex rodent nest, 16 km W of Beaver, 2134 m, 7 May 1949 (PHS). Garfield Co.: 1 male, 1 female, 6 km S of Panguitch, 2043 m (juniper), 29 April 1949. *Wyoming:* Albany Co.: 1 male, 1 female, ex *Neotoma cinerea*, 10 July 1944 (PHS); 3 females, ex *Neotoma* sp., 8 July 1943 (PHS).

Discussion: Anomiopsyllus n. starki, a nomen nudum described by Barnes in his doctoral dissertation in 1963, is the same in all morphological characters and measurements as *A. n. mexicanus*. *Anomiopsyllus n. mexicanus* represents a form intermediate between *A. n. nudatus* and *A. n. hiemalis*, as indicated by Barnes in his description of *A. n. starki*. Measurements (males) given by Barnes were based on specimens of *A. n. starki*.

Anomiopsyllus nudatus hiemalis Eads and Menzies n. comb.

Figs. 10, 34, 56, 69, 82, 94

Anomiopsyllus hiemalis Eads and Menzies, 1948, J. Kans. Ent. Soc. 21(4): 133-136; Eads and Menzies, 1950, Texas State Hlth. Dept. 53; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 11; Vargas, 1960, Med. Rev. Mexicana 40 (849) 1-4; Poorbaugh and Gier, 1961, J. Kans. Ent. Soc. 34(4): 200; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Pratt and Stark, 1973, DHEW Publ. 74-8267: 11.

Anomiopsyllus hiemalis hiemalis: Holland, 1965, Canadian Ent. 97: 1055-1056; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Males of *A. n. hiemalis* are distinguished from *A. n. nudatus* by the wide space between the distal pair of spiniforms on the movable process (greater than 20 u), and from *A. n. mexicanus* by the presence of a slender bristle at the arc of curvature of sternum IX. The movable process in *hiemalis* is shorter than in *nudatus* or *mexicanus* (M = 107 u, range 97 to 112 u), but broader than both (M = 81 u, range 73 to 94 u). The distance between the distal pair of spiniforms closely overlaps that of *mexicanus* (M = 35 u, range 16 to 42 u), but the two species may be distinguished by the thin bristle on sternum IX.

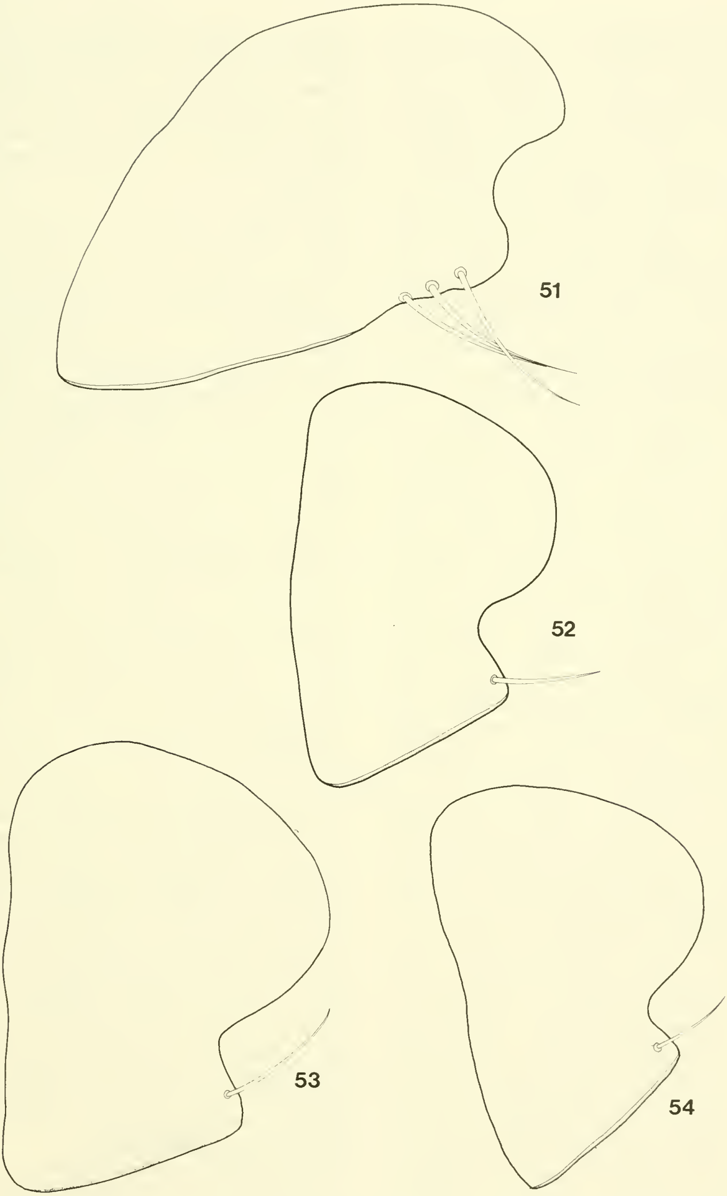
Female characters are not sufficiently distinctive to separate the subspecies of *A. nudatus*.

Type locality: Gaines County, Texas.

Type host: Neotoma micropus Baird

Type specimens: Male holotype and female allotype collected on 23 and 9 (respectively) April 1948 by V. I. Miles, deposited in U.S. National Museum.

Material examined: Colorado: Baca Co.: 1 male, 1 female, ex *Neotoma albigula*, 6 km N of Pritchett, 1341 m, 11 May 1948 (PHS). Pueblo Co.: 1 male, ex *Neotoma* sp., 6 August 1948 (PHS). Yuma Co.: 1 male, 1 female, ex *Neotoma albigula*, 1.6 km S, 6 km W of Wray, 1068 m, 10 July 1948 (PHS). *Kansas:* Barber Co.: 1 male, 1 female, ex *Neotoma micropus*, 5.6 km S, 1.6 km W of Aetna, 13 April 1949, Loomis and Lipovsky (RM); 18 males, 23 females, ex *Neotoma micropus*, 8 km S of Aetna, no date, Hopla and Loomis (U.O.); 41 males, 89 females, ex *Neotoma micropus*, Hopla (U.O.). Clark Co.: 1 male, 1 female, ex *Neotoma micropus*, 15 May 1942 (PHS). Gove Co.: 3 females, ex *Neotoma* sp., 7 September 1946 (PHS). Meade Co.: 1 female, ex *Neotoma micropus*, 12 May 1942 (PHS); 1 female, ex *Sigmodon hispidus*, 19 km S of Meade, 10 May 1950 (PHS). Seward Co.: 1 male, 1 female, ex *Neotoma micropus*, 15 May 1942 (PHS). *New Mexico:* Chavez Co.: 2 males, 2 females, ex *Neotoma albigula*, 8 km E of Haggerman, 1037 m (mesquite), 13 April 1948 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 11 km E of Haggerman, 1158 m, 8 April 1948 (PHS). Eddy Co.: 2 males, 2 females, ex *Neotoma albigula*, 8 km E of Artesia, 1158 m (mesquite), 24 March 1949 (PHS); 1 female, ex *Neotoma albigula*, 3 km W of Loco Hills, 1006 m (yucca, mesquite), 16 February 1950 (PHS). Lea Co.: 1 male, ex *Neotoma albigula*, 6 km N, 31 km E of Lovington, 1220 m, 25 March 1949 (PHS); 4 males, 4 females, ex *Neotoma* nest,.8 km N of Hobbs, 1006 m (mesquite), 22 February 1950 (PHS). *Oklahoma:* Caddo



Figs. 51-54. Male eight sternum: 51, *A. nidiophilus*; 52, *A. amphibolus*; 53, *A. montanus*; 54, *A. sinuatus*.

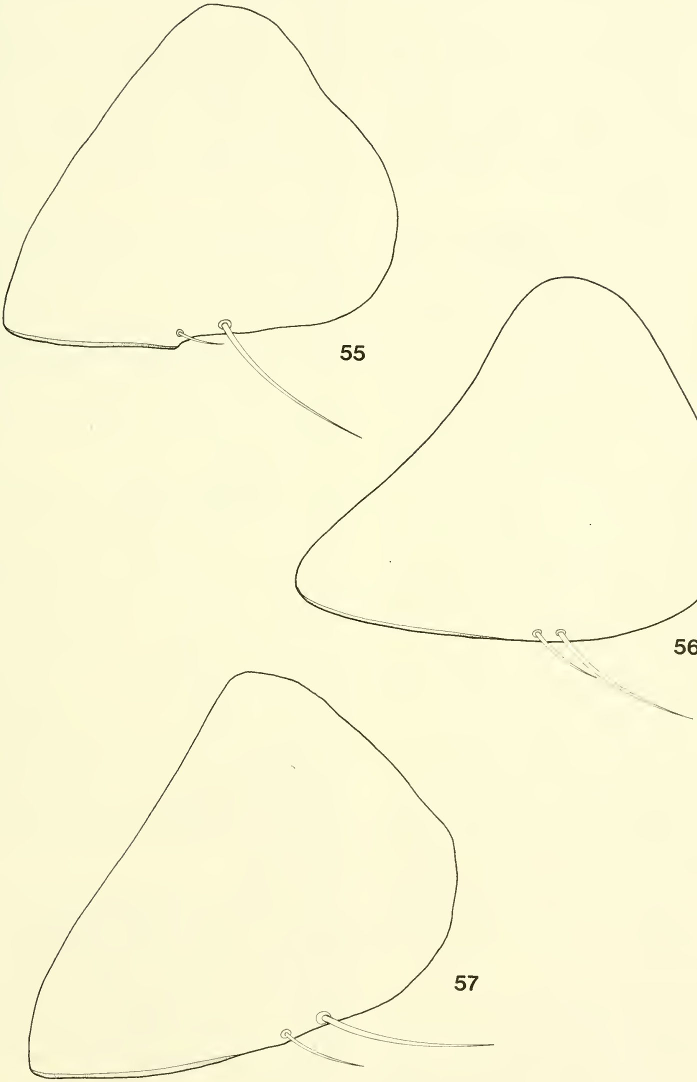
Co.: 2 males, 2 females, ex *Neotoma micropus* nest, April 1958, T. Emerson (U.O.). Herman Co.: 5 males, 16 females, ex *Neotoma micropus* nests, April 1960, C. J. Mitchell (U.O.). Texas Co.: 1 male, ex *Neotoma albigula*, 9.7 km E of Hardesty, 945 m (yucca, sagebrush), 9 May 1950 (PHS). *Texas:* Bailey Co.: 1 female, ex *Neotoma* sp., Muleshoe, 3 March 1957, Simmons. Brewster Co.: 1 male, ex *Neotoma mexicana*, 20 April 1942 (PHS); 2 females, ex rodent nest, Big Bend National Park, 31 October 1963, V. J. Tipton; 1 male, ex *Neotoma micropus* nest, Big Bend National Park, 2 November 1948, V. J. Tipton; 1 male, 1 female, ex *Peromyscus pectoralis*, Big Bend National Park, 10 April 1963, V. J. Tipton. Coke Co.: 3 females, 1 male, ex *Neotoma albigula*, 29 April 1942 (PHS). Crane Co.: 1 male, ex *Neotoma albigula*, 29 April 1942 (PHS). Dawson Co.: 1 male, 1 female, ex *Neotoma micropus*, 11 February 1948 (PHS); 1 female, ex *Neotoma micropus*, 2 November 1948, Miles. Ector Co.: 2 males, 1 female, ex *Neotoma floridana*, 26 km W of Odessa, 884 m (mesquite, yucca), 15 April 1960 (PHS). Hartley Co.: 4 males, 3 females, ex *Neotoma micropus*, October 1944 (PHS). Hutchinson Co.: 3 males, 1 female, ex *Neotoma micropus*, 31 May 1944 (PHS); 1 male, 1 female, ex *Neotoma micropus*, 9.7 km W of Electric City (mesquite), 2 May 1950 (PHS). Jeff Davis Co.: 1 male, 1 female, ex *Neotoma mexicana*, 2 May 1942 (PHS). Knox Co.: 1 male, 1 female, ex *Neotoma mexicana*, 16 October 1946 (PHS). Motley Co.: 1 male, 1 female, ex *Neotoma albigula*, 3 October 1946 (PHS). Pecos Co.: 1 male, ex *Dipodomys spectabilis*, 21 April 1942 (PHS). Terrell Co.: 1 male, ex *Neotoma albigula*, 1 April 1942 (PHS). Tom Green Co.: 3 males, 1 female, ex *Neotoma* sp., 11 April 1947 (PHS). Ward Co.: 2 males, 2 females, ex *Neotoma albigula*, 5 April 1948 (PHS). *Mexico:* Coahuila D. F.: 2 males, 2 females, ex *Neotoma micropus*, Sabinas, 20 September 1944, A. Dampf (RM); 1 male, 1 female, same locality, no date, T. Mazzotti (RM); 2 males, 2 females, same locality, 30 August 1944 (PHS); 1 male, 1 female, ex *Neotoma* nest, same locality, 1 October 1944 (RT).

Discussion: Eads and Menzies (1948) in describing *A. hiemalis* noted the close relationship to *nudatus*, and differentiated their species primarily by the greater distance between the distal spiniforms of the movable process in *hiemalis*. They stated that the movable process is "... broad and conical." The breadth of the process was considered diagnostic.

Stark (1959) reported the existence of atypical *nudatus* in western Utah, noting the greater distance between spiniforms in his atypical specimens as compared to the typical *nudatus*. Stark also noted that sternum IX of males in his atypical specimens varied from typical *nudatus*, but did not give any details. *Anomiopsyllus nudatus mexicanus* is intermediate between *A. nudatus nudatus* and *A. nudatus hiemalis* with respect to distance between spiniforms, but distinct from either by virtue of several modified setae dorsomedially on the posterior margin of male sternum IX. It is also intermediate geographically, its range falling between the eastern *hiemalis* and the western *nudatus*. In regard to length and breadth of the movable process, *A. n. mexicanus* is more like *nudatus* than like *hiemalis*. The process of *mexicanus* is apparently longer in relation to width than that of *hiemalis*, thus less "conical."

Exhaustive examination of specimens available for study has not resulted in finding characters other than those mentioned. The morphology of the populations is subject to remarkably little variation except in the male external genitalia. Other possible characters thoroughly investigated were: setation of head, thorax, and abdomen; shape of thoracic segments and setation of legs; potential difference in proportion of tarsal segments; and both male and female genitalia. No other consistent variations were found. The females are apparently not separable, although a trend exists toward a deeper sinus in the posterior margin of tergum VIII of *A. n. hiemalis*. The sinus is used as a key character for *hiemalis* by Hopkins and Rothschild (1962).

To examine the relationships of the three groups, a series of measurements was taken as follows: (1) width of the movable process



Figs. 55-57. Male eight sternum: 55, *A. nudatus nudatus*; 56, *A. nudatus hiemalis*; 57, *A. nudatus mexicanus*.

from the "notch" above the point of articulation across the broadest portion of the lower lobe; (2) length of the process from its tip to the "notch"; (3) distance from center to center between the spiniforms. The manner in which measurements were made is illustrated in Figure 93. The measurements were taken with a calibrated ocular grid, using 10X eyepiece and 43X objective with grid units converted to microns (0.1 grid units = 1.624 u).

Due to the allopatric nature of the populations, *mexicanus*, the geographically central population, was compared first to *hiemalis* and then to *nudatus*. If each of the two populations is related to *mexicanus*, then they are related to one another. *Anomiopsyllus n. mexicanus* and *hiemalis* are closely linked by the overlap of distances between spiniforms, yet separated by length and width of the movable process. *Anomiopsyllus n. mexicanus* and *nudatus* are sharply distinguished by distance between spiniforms, but with significant overlap in length of process, and they almost completely overlap in width of process. *Anomiopsyllus n. mexicanus* is further distinguished from both *hiemalis* and *nudatus* by presence of modified setae (Figs. 24, 25) of sternum IX in males.

The *A. nudatus* complex ranges from western Kansas, Oklahoma, and Texas south to Sabinas, Coahuila, Mexico, and west to the Pacific Coast of southern California.

The subspecies *A. nudatus nudatus*, the westernmost representative of the three subspecific populations, has a primarily Sonoran Desert distribution (Shreve and Wiggins 1951; Map 2). Its range is not limited to the Sonoran Desert, but occurs in a variety of habitats occupied by its wood rat hosts; e.g., in pine-fir forest at 2134 m elevation in the San Bernardino Mountains of southern California.

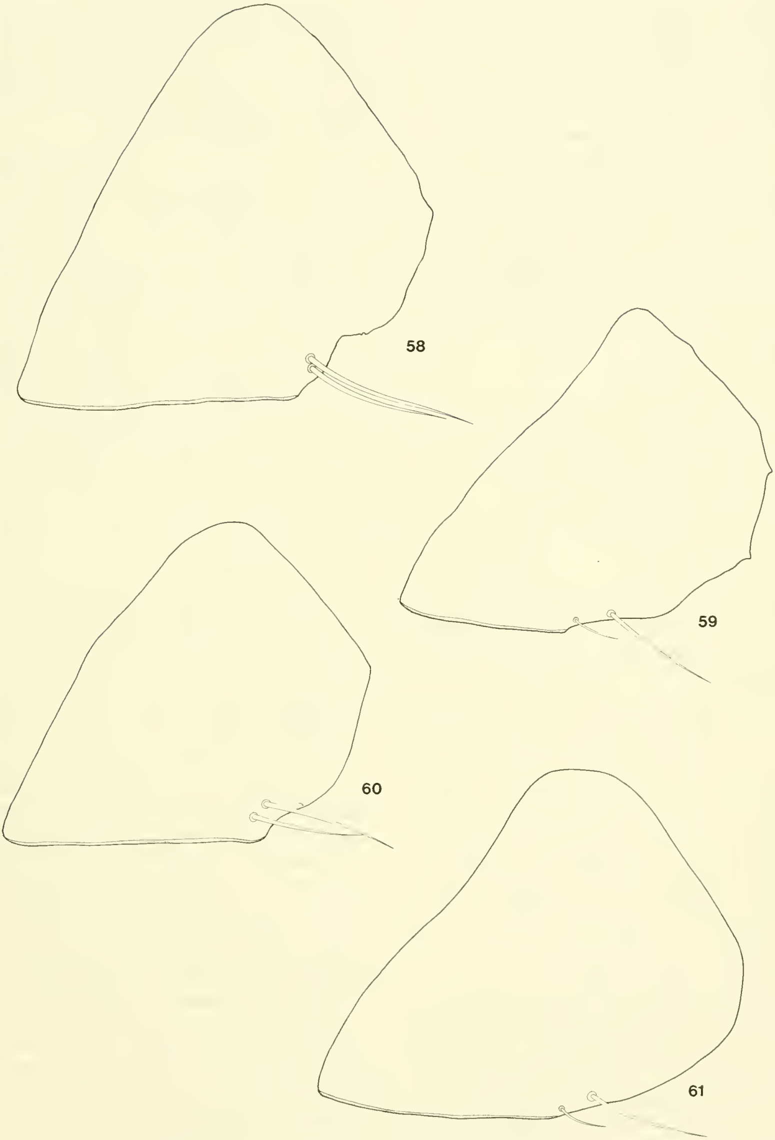
In southern California, *A. n. nudatus* is found in coastal chaparral and oak woodland bordering the sea as well as in its typical desert habitat. In the Santa Monica Mountains and parts of the San Gabriel Mountains of Los Angeles County, it is replaced by *A. falsicalifornicus* in moister oak woodland and chaparral situations. In the Los Angeles area, the distributions of *A. n. nudatus* and *A. falsicalifornicus* interdigitate: *nudatus* occurs in drier areas where yucca and cactus grow, and *falsicalifornicus* occurs in moister areas characterized by *Rhus diversiloba* and *Photinia*. This situation continues northward to Ventura County, California, where *nudatus* occupies the arid habitat in the rain shadow south and east of the southern Santa Ynez Mountains.

From Ventura County eastward, *nudatus* is recorded from the area of Frazier Park, Kern County, and the Antelope Valley of northern Los Angeles County. It is replaced above the lower, winter snow line by *A. walkeri* in the Tehachapi and southern Sierra Nevada Mountains. From this point it occurs across the Mojave and Sonoran deserts, its distribution including the southwest corner of Nevada and Sonoran Desert areas of Arizona.

Areas where the distribution of *n. nudatus* is doubtful include the northern portions of the Mojave Desert and arid areas on the west side of the southern San Joaquin Valley in California where collections of wood rat nests made by the senior author have been negative for *Anomiopsyllus*. Several females, collected by R. Ryckman from the San Pedro Martir Mountains of Baja California, are probably *A. n. nudatus*. A collection of 20 wood rats (*Neotoma albigula*) near Hermosillo, Sonora, Mexico, by K. Murray and H. Johnson during March and April, 1960, failed to produce *Anomiopsyllus*. *Anomiopsyllus n. mexicanus* was collected in central Mexico by J. E. H. Martin during July 1964 from a nest of *Neotoma* sp.

In Arizona, the distribution of *A. n. nudatus* is sharply interrupted along the escarpment of the Colorado Plateau by the presence of a central subspecies, *A. n. mexicanus*. In San Juan County, southeastern Utah, *A. n. nudatus* makes a deep incursion into the area occupied by *A. n. mexicanus* (Map 2), a situation further discussed under that subspecies.

The distribution of *A. nudatus mexicanus* lies within the Basin and Range Province as defined by Shreve and Wiggins (1951). In



Figs. 58-61. Male eight sternum: 58, *A. falsicalifornicus congruens*; 59, *A. walkeri*; 60, *A. falsicalifornicus falsicalifornicus*; 61, *A. martini*.

Arizona, its boundaries coincide with the edge of the Sonoran Desert and the occurrence of *A. nudatus nudatus*. In the east, its range is interrupted by the western edge of the Great Plains (High Plains, according to Webb 1951) and the presence of *A. n. hiemalis*. Its northern range is indented by the central Rocky Mountain mass. A narrow band just east of the Rockies carries the subspecies through far eastern Colorado and western Kansas to Morrill County, Nebraska, and Albany County, Wyoming. In southcentral New Mexico, it is absent from the lower Chihuahuan Desert habitat, where it is replaced by *A. novomexicanensis*, as *A. n. mexicanus* appears to occupy the higher elevations.

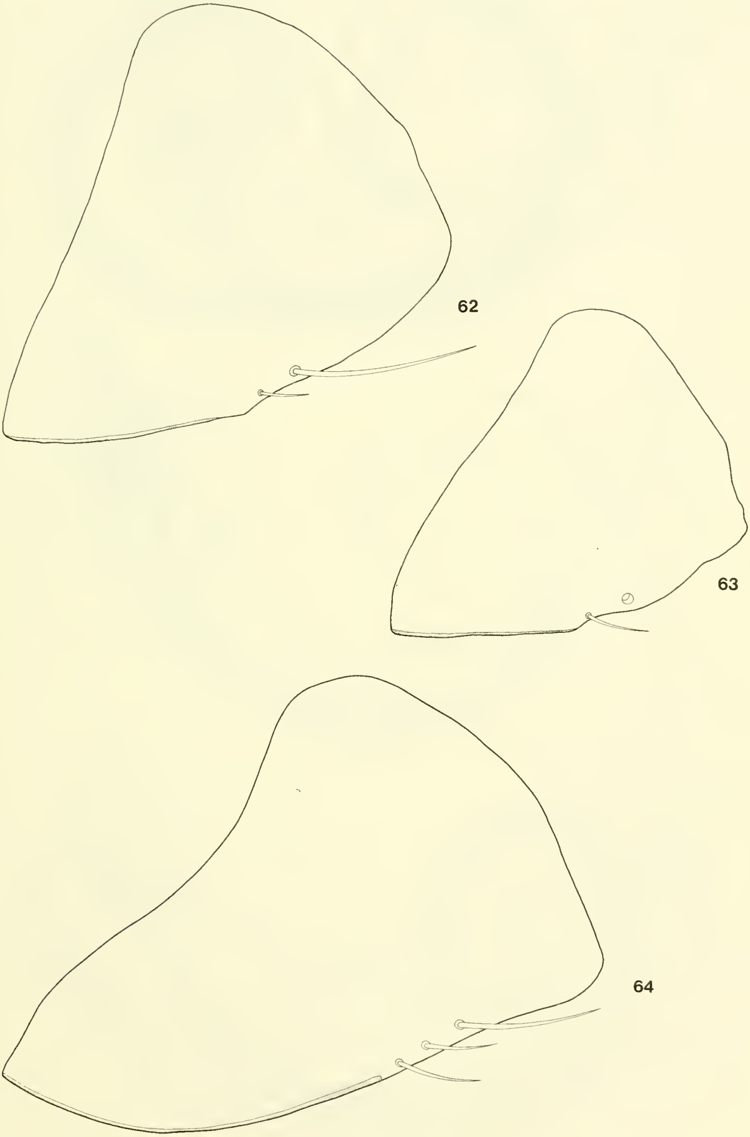
In Utah, a confusing picture is presented by the occurrence of *nudatus nudatus* in San Juan County in the southeastern corner of the state. Stark (1959) reported atypical *nudatus* from Millard, Beaver, and Garfield counties in Utah and typical *nudatus* in San Juan County. Examination of his specimens shows the former to be *n. mexicanus* and the latter *n. nudatus*. It is suspected that barriers such as the Colorado River in the west and discontinuous wood rat distribution to the east may explain the disjunct distribution observed in *n. nudatus*. In San Juan County, only *n. nudatus* has been collected; however, west of the Colorado River in Utah, only *n. mexicanus* has been collected. Two of the San Juan *n. nudatus* collections are from high elevations in habitats similar to those preempted by *n. mexicanus* along the Colorado Plateau escarpment where the two subspecies are known to meet. Collections in the rugged area of southcentral Utah and northcentral Arizona are needed to clarify the *n. mexicanus* distribution.

Anomiopsyllus n. hiemalis replaces *A. n. mexicanus* at lower elevations at the eastern and southwestern edge of the *n. mexicanus* distribution. The distributions of the two subspecies interdigitate where plains are intersected by spurs of the Rockies (see *novomexicanensis* for further discussion). Intergrades between *n. mexicanus* and *n. hiemalis* occur in Santa Fe and San Miguel counties, New Mexico, and specimens assignable to each subspecies have been taken in the same area in Santa Fe County by U.S.P.H.S. field workers. In eastern New Mexico and Colorado where apparent overlap occurs, *n. hiemalis* occupies the habitat below 1341 m elevation and *n. mexicanus* occupies the higher elevations.

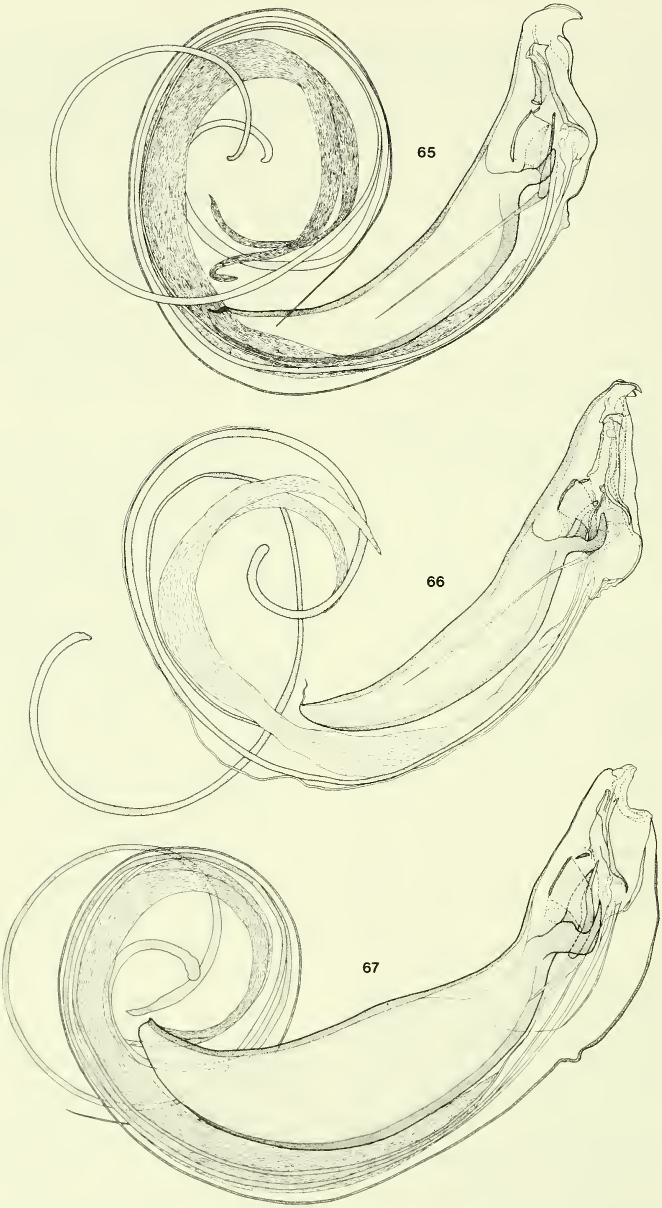
The range of *A. n. hiemalis* falls primarily into two biotic areas defined by Webb (1951) as the High Plains and Trans-Pecos areas and by Dice (1943) as the Kansan and Tamaulipan. These areas are characterized by moderate elevation (generally below 1220 m) and low annual rainfall (50 cm or less). Where vegetation type has been noted on *n. hiemalis* slides examined, mesquite (*Prosopis* sp.) predominates. Geographically, the area occupied by *n. hiemalis* includes southwestern Kansas, western Oklahoma and Texas, extreme eastern Colorado, and New Mexico south to Sabinas, Coahuila D. F., Mexico. The northernmost record noted is Yuma County, Colorado, and the easternmost are Barber County, Kansas, and Caddo County, Oklahoma.

As was speculated earlier for *n. nudatus*, the ranges of all three subspecies probably extend south into Mexico. The lack of specimens from Mexico precludes an accurate estimate, but the habitats occupied in the United States also occur in Mexico. Shreve and Wiggins (1951) shows Sonoran Desert, the habitat occupied by *n. nudatus*, as occurring west of the Sierra Madre Occidental as far south as the Río Yaqui. The upland habitat preferred by *n. mexicanus* extends south along the continental divide (Brand 1936, Leopold 1950). The mesquite scrub, characteristic of *n. hiemalis* habitat in Texas, extends south into eastern Mexico.

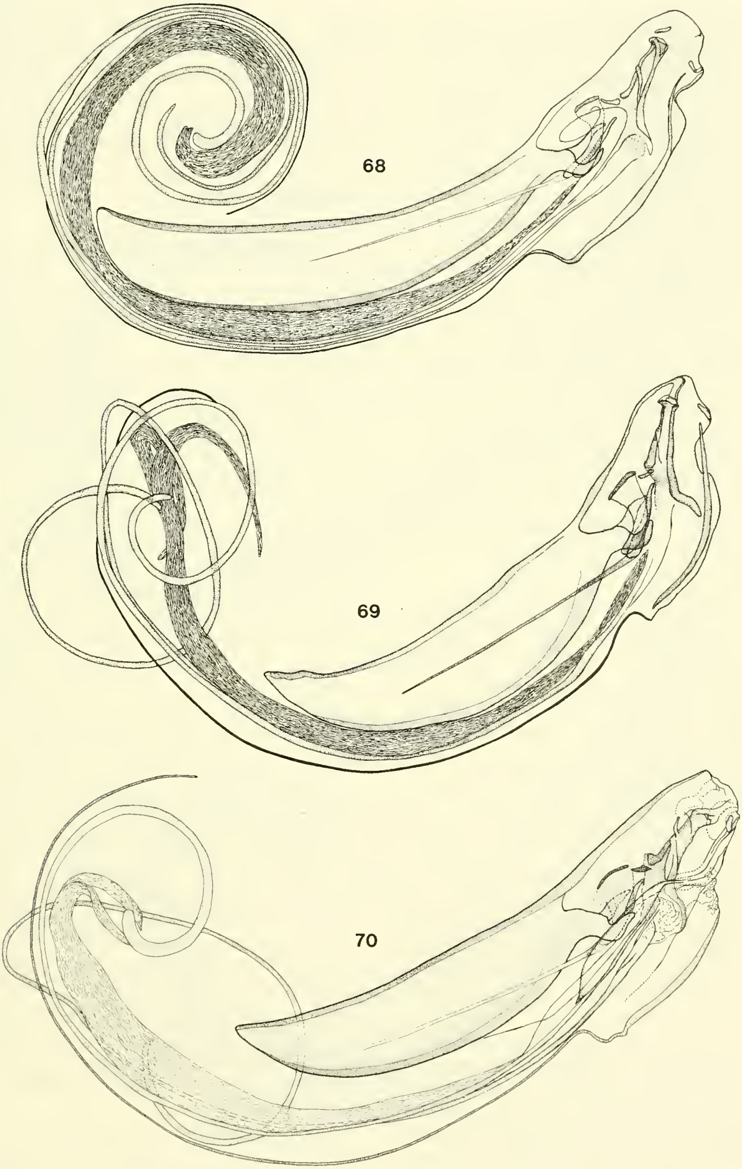
The apparent replacement of one subspecies by another with great changes in topography and habitat is strongly suggestive of similar phenomena noted with other *Anomiopsyllus* species. In California, where extensive field collecting was done in this study, *A. nudatus* was found to be replaced by *A. walkeri* at higher elevations in the Tehachapi Mountains and by *A. falsicalifornicus* in more mesic environments (i.e., rainfall over 50 cm/year). The phenomenon of displacement may be understood ultimately



Figs. 62-64. Male eight sternum: 62, *A. novomexicanensis*; 63, *A. durangoensis*; 64, *A. oaxacae*.



Figs. 65-67. Aedeagus: 65, *A. sinuatus*; 66, *A. montanus*; 67, *A. nidiophilus*.



Figs. 68-70. Aedeagus: 68, *A. nudatus nudatus*; 69, *A. nudatus hiemalis*; 70, *A. nudatus mexicanus*.

through laboratory studies or the range of tolerance for physical climate factors or by further field studies involving several of the species. The response to climate is not the only limiting factor involved in distribution of *Anomiopsyllus* species. This is illustrated by those species or subspecies that are capable of occupying a broad spectrum of climatic conditions in the absence of related species or subspecies. *Anomiopsyllus n. nudatus* occurs at elevations up to 2195 m in California and is displaced by *A. n. mexicanus* at higher elevations in Arizona and *A. walkeri* in California as noted above.

Hosts: Anomiopsyllus nudatus subspecies are restricted to wood rats (*Neotoma* spp.) as major hosts and seldom occur on other rodents. In the material examined, fortuitous hosts are probably more numerous than normally occur in nature. Many of these records result from plague surveys in which most of the specimens were ground and inoculated into test animals, and collectors often tended to retain specimens from odd hosts for the record.

Within the habitats occupied by *A. nudatus*, its subspecies occur indiscriminately on available wood rat species, with the exception of *Neotoma cinerea* which Goldman (1910) and Hall and Kelson (1959) place in a separate subgenus, *Teonoma*. *Neotoma floridana* is primarily a resident of moist eastern deciduous forest communities. Its distribution extends through western Kansas and northeastern Colorado where it occupies situations characteristic of *N. albigula* such as cactus huts (Warren 1942). In Colorado, Finley (1958) has recorded *Anomiopsyllus* sp. from *N. floridana*, but his specimens have not been available for study. On the other hand, Rainey (1956), and Ellis (1955) did not record *Anomiopsyllus* from *N. floridana* in eastern Oklahoma.

The range of *A. nudatus* or any of its subspecies never coincides with the range of any one wood rat species. Thus, in southern California, *nudatus nudatus* occurs on both *N. lepida* and *N. fuscipes* in arid situations, while in less arid areas the same two hosts are parasitized by different *Anomiopsyllus* species. In Arizona and New Mexico the range of *N. mexicana* appears to limit the range of *A. n. mexicanus*, but the *N. mexicana* range is exceeded by the range of *A. n. mexicanus* in western Utah where the flea occurs on *N. lepida*. Within the range of the host genus *Neotoma*, *A. nudatus* subspecies are apparently limited by factors other than host occurrence as are other *Anomiopsyllus* spp.

Anomiopsyllus falsicalifornicus Fox

Figs. 14, 15, 37, 40, 58, 60, 71, 72, 85, 86, 95

Anomiopsyllus californicus: Fox, 1926 (*nec* Baker, 1904), Pan-Pacific Ent. 2: 183; Wagner, 1930, Mag. Parasitol. Moscow 1: 135.

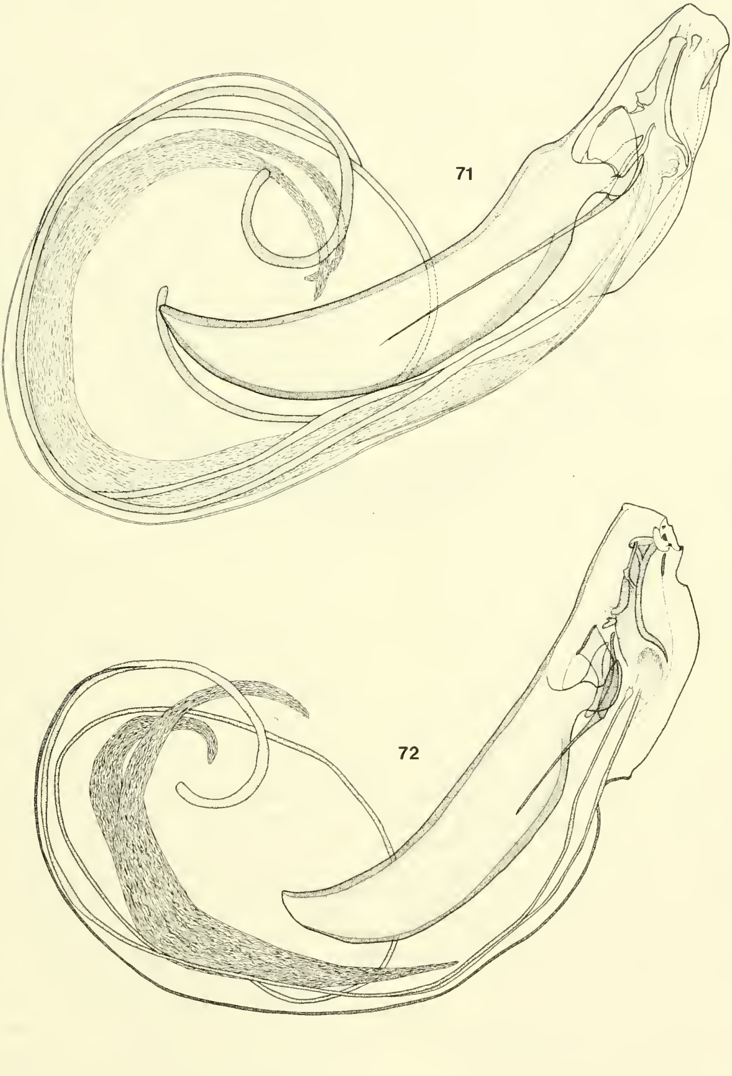
Anomiopsyllus falsicalifornicus Fox, 1929, Ent. News 40: 218; Collins, 1936, Ent. News 47: 130; Hubbard, 1947, Fleas of western North America: 78-80; Linsdale and Davis, 1956, Univ. Calif. Publ. Zool. 54: 306-308; Holland, 1965, Canadian Ent. 97: 1052; Barnes, 1965, Pan-Pacific Ent. 41(4): 278; Coultrip et al., 1973, J. Med. Ent. 10(3): 306.

Diagnosis: Anomiopsyllus falsicalifornicus is separable from other species (males) by the suboblique row of three spiniform setae near the apex of the movable process coupled with the presence of only 0-3 spiniforms at the apex of the distal arm of sternum IX. The movable process is roughly triangular with always some degree of concavity (shallow to extreme) on the posterior margin below the distal spiniform row. The anterior margin is linear, tipped slightly anterad at the subacute apex with three heavy spiniforms near the apex with or without a small spiniform near the posterior margin of the basal lobe. The proximal arm of sternum IX is similar to *nudatus*. The distal arm is variable in shape and the apex rounded or flattened with 0-3 heavy setae at the apex and a row of 4-6 moderately heavy setae mesad on the posterior margin.

Females are similar to *nudatus* but can be separated by the presence of the sclerotized portion of the blind ductus seminalis (Fig. 72, 76). Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus*.

Average Length: Male 1.6 mm; female 1.9 mm.

Type locality: Claremont, Los Angeles County, California



Figs. 71-72. Aedeagus: 71, *A. walkeri*; 72, *A. martini*.

Type host: Neotoma fuscipes and *Spilogale phenax*

Type specimens: Male holotype deposited in the U.S. National Museum.

Fox (1926) first described the male of this species, believing it to be *A. californicus* Baker, a species that had been described from near Claremont, California. Jordan and Rothschild (1915) examined Baker's syntypic series of females and entered *californicus* into synonomy with *nudatus.* Fox (1929), acting on information from Jordan, then gave his male specimen the name *falsicalifornicus.*

Anomiopsyllus falsicalifornicus is treated here as two subspecies: *A. f. falsicalifornicus, A. f. congruens.*

Anomiopsyllus falsicalifornicus congruens Stewart

Figs. 15, 40, 58, 71, 85, 95

Anomiopsyllus congruens Stewart, 1940, Pan-Pacific Ent. 16: 17-18; Hubbard, 1940, Pac. Univ. Bull. 37(4); Hubbard, 1943, Pac. Univ. Bull. 39(8): 1-12; Augustson, 1943, Bull. South. Calif. Acad. Sci. 42: 69; Hubbard, 1947, Fleas of western North America: 81–82; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Linsdale and Davis, Univ. Calif. Publ., Zool. 54(5): 306-308; Holland, 1965, Canadian Ent. 97: 1052, Barnes, 1965, Pan-Pacific Ent. 41(4): 278.

Anomiopsyllus falsicalifornicus congruens Hopkins, 1952, J. Wash. Acad. Sci. 42(11): 365; Holland 1965, Can. Ent. 97: 1053; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2-13: 19; Lewis 1974, J. Med. Ent. 11(2): 154.

Diagnosis: The males of *A. f. congruens* are distinguished from *A. f. falsicalifornicus* by the narrow sternum IX with an angulate, truncate apex. The fixed process of the clasper is broader than long. Sternum IX is only one-third to one-half as broad mesally as in *f. falsicalifornicus* and is equipped apically with 1, 2, or 3 heavy setae. The movable process is similar to *f. falsicalifornicus* but possesses a proximal spiniform.

Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus.*

Type locality: Frances Simes Hastings Natural History Reservation near Jamesburg, Monterey County, California.

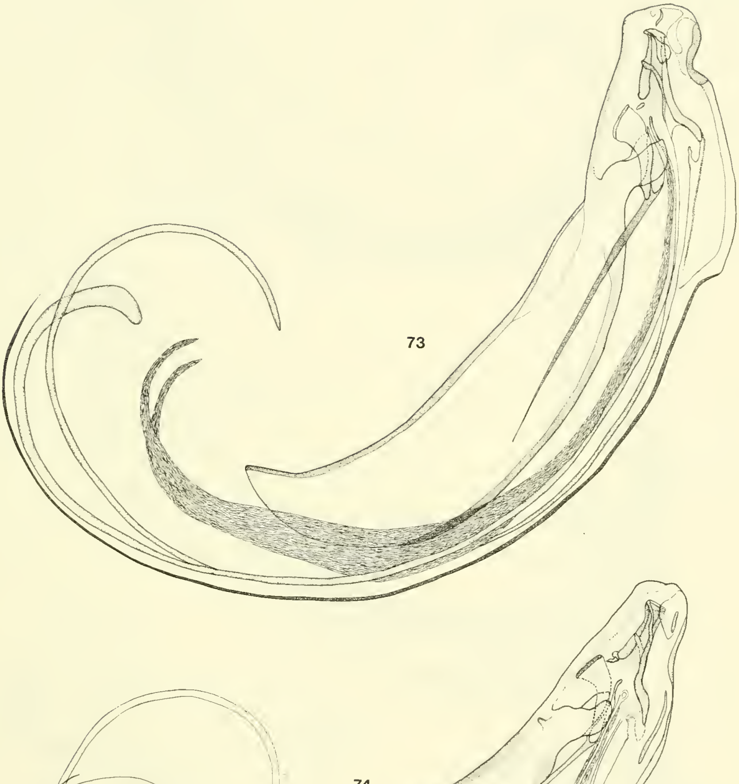
Type host: Spilogale gracilis ssp.

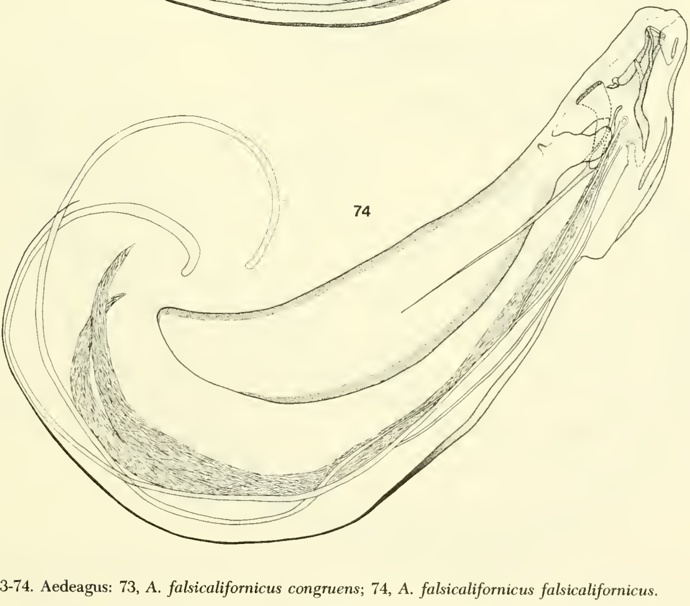
Type specimens: Holotype male and allotype female collected on 19 November 1938 by R. Holdenried, deposited in Museum of the California Insect Survey, Univ. of California, Berkeley, California.

Recorded distribution: California: Monterey Co. (type locality), San Luis Obispo Co. (Linsdale and Davis).

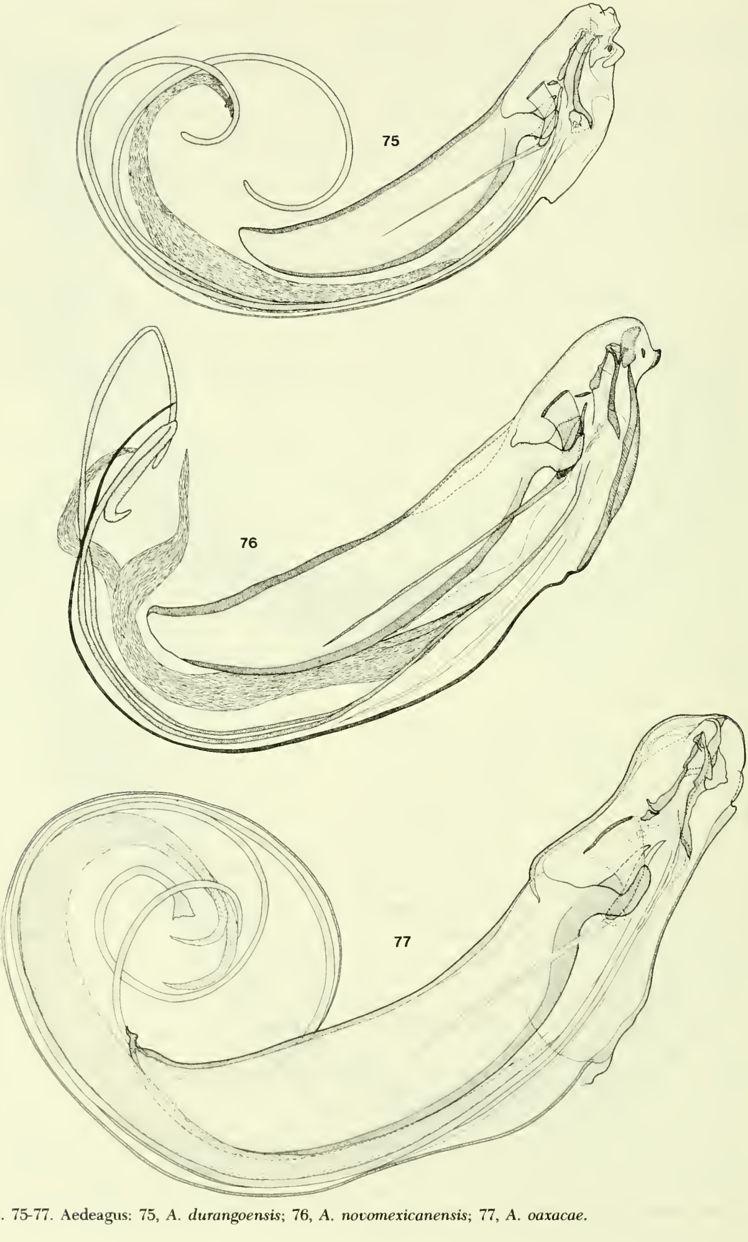
New distribution: From Santa Ynez Mountains of Santa Barbara Co. north to Siskiyou Co., thence south to the western Sierra Nevada foothills to Tulare Co., California.

Material examined: California: Alameda Co.: 1 male, 1 female, ex *Neotoma fuscipes*, Oakland (oak woodland), 1 July 1936 (RM); 27 males, 43 females, ex *Neotoma fuscipes* nests, Berkeley (oak woodland), 17 October 1959, Barnes (BVC). Amador Co.: 1 male, 3 females, ex *Neotoma fuscipes* nest, 1.6 km N, 5 km E of Plymouth (oak woodland), 14 January 1959, Barnes (BVC). Contra Costa Co.: 3 males, 7 females, ex *Neotoma fuscipes* nests, Orinda (oak woodland), 18 October 1959, Barnes (BVC). El Dorado Co.: 27 males, 43 females, ex *Neotoma fuscipes* nest, Placerville vicinity (oak woodland), many dates, Barnes (BVC); 110 males, 110 females, ex *Neotoma fuscipes* nest, Shingle Springs vicinity, many dates, Barnes (BVC). Fresno Co.: 4 males, 10 females, ex *Neotoma fuscipes* nest, 3 km N, 2 km W of Auberry (oak woodland), 7 January 1958, Barnes (BVC); 2 males, 6 females, ex *Neotoma fuscipes* nest, 1.6 km SW of Prather (oak woodland), 13 November 1958, Barnes (BVC). Lassen Co.: 1 male, 4 females, ex *Neotoma fuscipes* nest, 5 km NW of Little Valley (oak, *Ceanothus*, sagebrush), 6 May 1960, Barnes (BVC). Monterey Co.: 1 female, ex *Neotoma fuscipes*, Hastings Nat. Hist. Res., 14 July 1938 (RM); 1 male, 2 females, ex *Neotoma fuscipes*, 4 km E of Carmel, 21 December 1948, Holm (BVC); 1 female, ex *Eutamias merriami*, Hastings Nat. Hist. Res., 8 February 1947 (PHS); 1 male, ex *Perognathus californicus*, same locality, 18 January 1947 (PHS). Napa Co.: 1 male, ex *Neotoma fuscipes*, 4 km N, 2 km E of Calistoga (oak woodland), 24 October 1956, Murray (BVC). Nevada Co.: 3 males, 9 females, ex *Neotoma fuscipes* nest, 19 km S of Grass Valley (oak woodland), 15 January

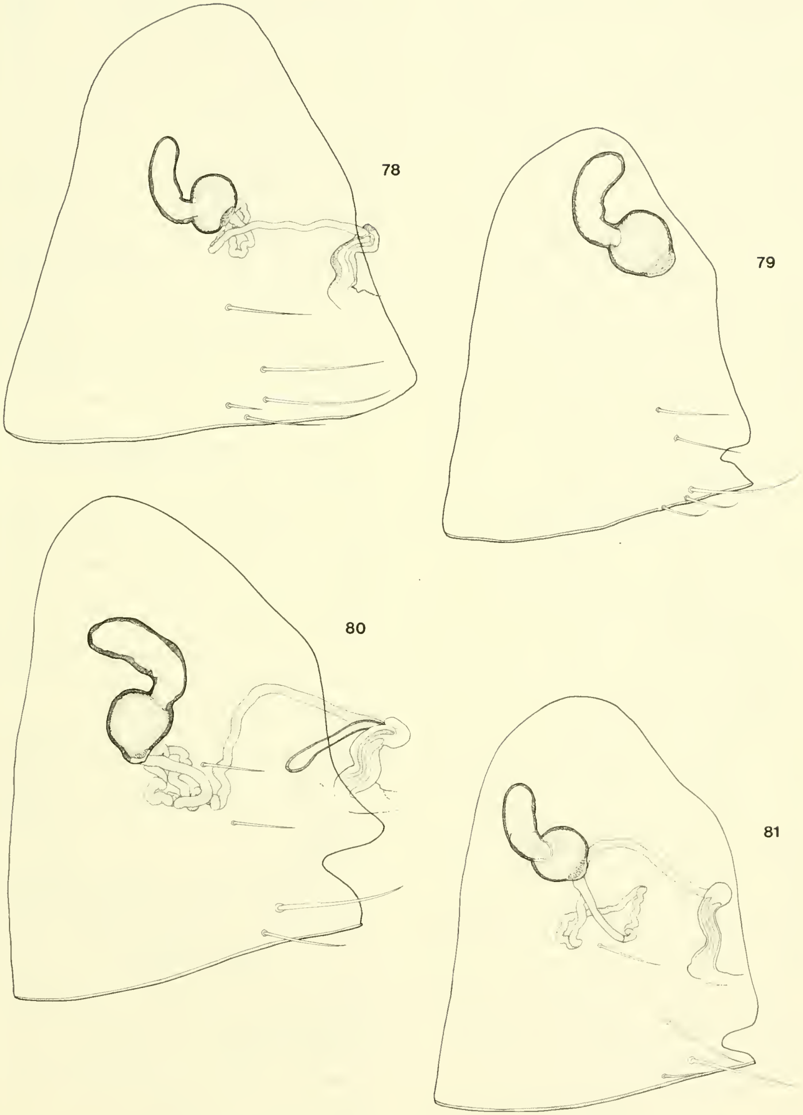




Figs. 73-74. Aedeagus: 73, *A. falsicalifornicus congruens*; 74, *A. falsicalifornicus falsicalifornicus*.



Figs. 75-77. Aedeagus: 75, *A. durangoensis*; 76, *A. novomexicanensis*; 77, *A. oaxacae*.



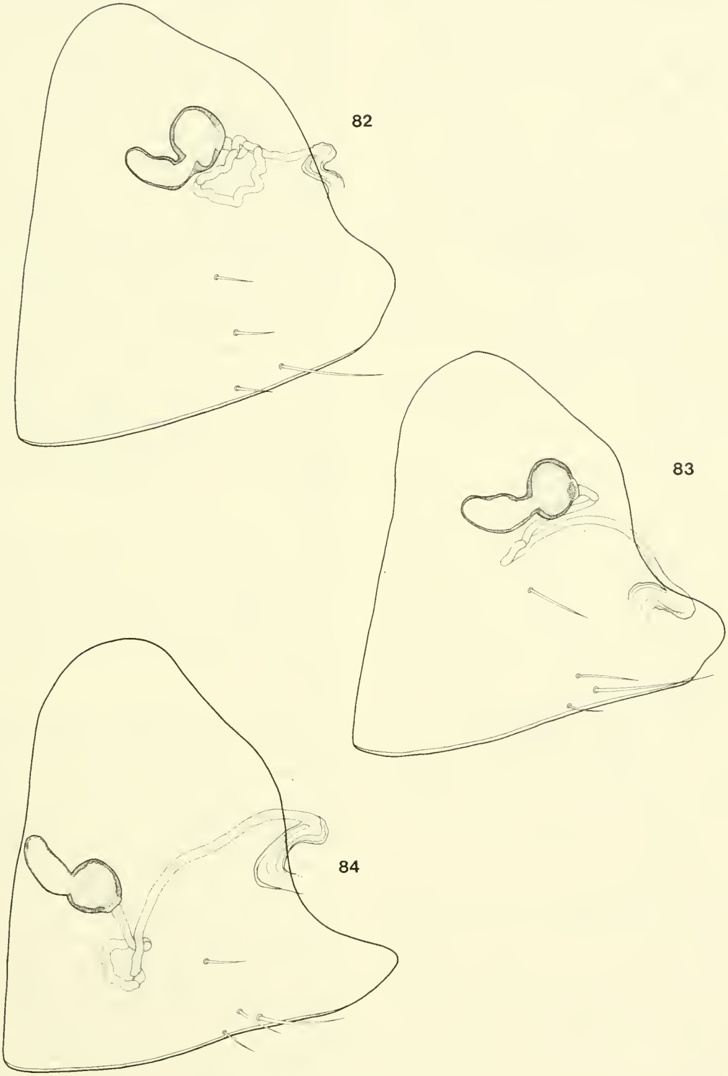
Figs. 78-81. Female seventh sternum and spermatheca: 78, *A. nidiophilus*; 79, *A. sinuatus*; 80, *A. amphibolus*; 81, *A. montanus*.

1959, Barnes (BVC). Plumas Co.: 17 males, 33 females, ex *Neotoma fuscipes* nest, 3 km W of Virgillia, 17 October 1961, Barnes. San Benito Co.: 2 males, ex *Neotoma fuscipes*, T14S R6E Section 2, 13 February 1951, Kirkwood (BVC). San Francisco Co.: 1 male, ex *Spermophilus beecheyi*, San Francisco (laboratory), no date (PHS). San Luis Obispo Co.: 7 males, 19 females, ex *Neotoma fuscipes* nest, 5 km N, 7.2 km E of Santa Margarita (oak woodland), 2 November 1956, Barnes (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, 1.6 km N, 6 km E of Santa Margarita (oak woodland), 15 June 1956, Barnes (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, same locality (oak woodland), 5 March 1957, Barnes (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, 1.6 km N, 6 km E of Santa Margarita (oak woodland), 1 November 1956, Murray (BVC); 1 male, 6 females, ex *Neotoma fuscipes* nest, 5 km N of Pozo (chaparral, woodland), 20 November 1956, Barnes (BVC); 3 males, 1 female, ex *Neotoma fuscipes*, La Panza Camp (chaparral), 3 June 1955, Murray (BVC); 1 male, 1 female, ex *Neotoma fuscipes*, San Luis Obispo, 1 June 1935 (RM); 1 male, ex *Peromyscus boylei*, 1.6 km N, 4 km E of Santa Margarita (oak woodland), 15 June 1956, Murray (BVC); 1 male, 2 females, ex *Peromyscus truei*, same locality (oak woodland), 15 June 1956, Murray (BVC); 1 male, ex *Peromyscus truei*, 3 km N, 6 km E of Pozo (chaparral), 7 March 1957, Barnes (BVC); 1 female, ex *Microtus californicus*, 3 km E of Cayucos, 1 June 1947, Ryan and Durham (HF). San Mateo Co.: 1 female, ex *Neotoma fuscipes*, La Honda, 26 March 1949, Prince (PHS). Santa Barbara Co.: 3 males, 4 females, ex *Neotoma lepida*, Buckhorn Canyon, 6 km E of Santa Maria (chaparral), 24 April 1957, Barnes, Murray (BVC); 1 male, ex *Neotoma fuscipes*, Lompoc (oak woodland, chaparral), 9 February 1961, Rohe (BVC); 31 males, 53 females, ex *Neotoma fuscipes* nests, same locality, 9 February 1961, Rohe (BVC); 11 males, 18 females, ex *Neotoma fuscipes* nests, 47 adults reared from larvae 9 km N, 11 km W of Santa Barbara (oak, chaparral), 8 May 1961; 43 males, 74 females, ex *Neotoma fuscipes* nests, San Marcos Pass, 12 km N, 13 km W of Santa Barbara (oak woodland), 8 May 1961, Barnes. Santa Clara Co.: 1 male, 1 female, ex *Neotoma fuscipes*, Los Gatos, 24 June 1936 (RM). Santa Cruz Co.: 2 males, 1 female, ex *Neotoma fuscipes* nest, Boulder Creek, 305 m, 30 May 1939, Good (BVC); 1 male, 5 females, ex *Neotoma fuscipes*, same locality, 4 July 1940, Good (PHS). Siskiyou Co.: 2 males, 7 females, ex *Neotoma fuscipes* nest, 5 km W of Dorris (oak, pine), 6 April 1960, Barnes (BVC); 3 males, 6 females, 8 km S, 10 km W of Gazelle (juniper, oak), 2 April 1960, Barnes (BVC). Tulare Co.: 1 male, 2 females, ex *Neotoma fuscipes* nest, 1 km N, 5 km E of Lemon Cove (oak woodland), 2 April 1959, Barnes (BVC). Tuolumne Co.: 8 males, 17 females, ex *Neotoma fuscipes* nests, La Grange, 11 March 1958, Barnes and Keh (BVC).

Discussion: Stewart (1940) described *A. congruens* as a full species related to *A. falsicalifornicus*. Hopkins (1952) reduced *congruens* to subspecific status under *falsicalifornicus*, but his reasons weren't given. Linsdale and Davis (1956) presented a substantial case for full specific status for *A. congruens*, demonstrating constant morphological differences between the two forms. Hopkins and Rothschild (1962) held to the view of Hopkins (1952) and kept *congruens* at the subspecific level.

The view of Hopkins is amply supported by morphological, distributional, and reproductive data from this study. This, with the perspective gained from study of the genus as a whole, calls for subspecific assignment of *congruens*.

Morphologically, males of *A. f. congruens* and *A. f. falsicalifornicus* are immediately separable by the shape of the distal arm of sternum IX. In all of the *f. congruens* examined, this structure was narrow and angulate, truncate apically. In *Anomiopsyllus f. falsicalifornicus*, this structure is broader and gently rounded at the apex (Fig. 31). In the south coastal area of California where distributions of the two forms nearly meet, sternum IX of *f. congruens* has two large spiniform setae at the apex and *f. falsicalifornicus* has only one spiniform of moderate size with occasionally a small tacklike seta



Figs. 82-84. Female seventh sternum and spermatheca: 82, *A. nudatus hiemalis*; 83, *A. nudatus mexicanus*; 84, *A. nudatus nudatus*.

immediately below it. In the central Sierra Nevada Mountains populations of *f. congruens*, the number of apical spiniforms on this structure is reduced until, finally, in Tulare County, there are none in some local populations. Specimens with three spiniforms on the finger are occasionally found in more northern coastal populations. The shape of sternum IX remains constant.

Since Fox's (1926) description of *falsicalifornicus* and Stewart's (1940) description of *congruens*, the shape of the movable process has been considered diagnostic for the two groups. Stewart's description of *congruens* emphasized the lack of an apparent distal dilation of the process that he had observed in *falsicalifornicus*. In reality, the apparent dilation is due to a broad concavity of the posterior margin of the movable process, below which there is a broad, lightly sclerotized lobe (Figs. 12, 16). This concavity occurs to some degree in both *f. congruens* and *f. falsicalifornicus*. There is a tendency for more concavity in the process of *f. falsicalifornicus*, but some specimens of *f. congruens* are as deeply concave. A number of authors have erred in drawing and describing this structure, including Fox (1926), Stewart (1940), and Hubbard (1947). These authors failed to include the proximal lobe, an oversight that changes the appearance of the structure considerably. Linsdale and Davis (1956) simply did not illustrate its lower portion. Wagner (1936) illustrated the structure correctly, as did Collins (1936) in his supplementary description of *falsicalifornicus*. The overlap in shape of the movable process reduces its importance as a taxonomic character.

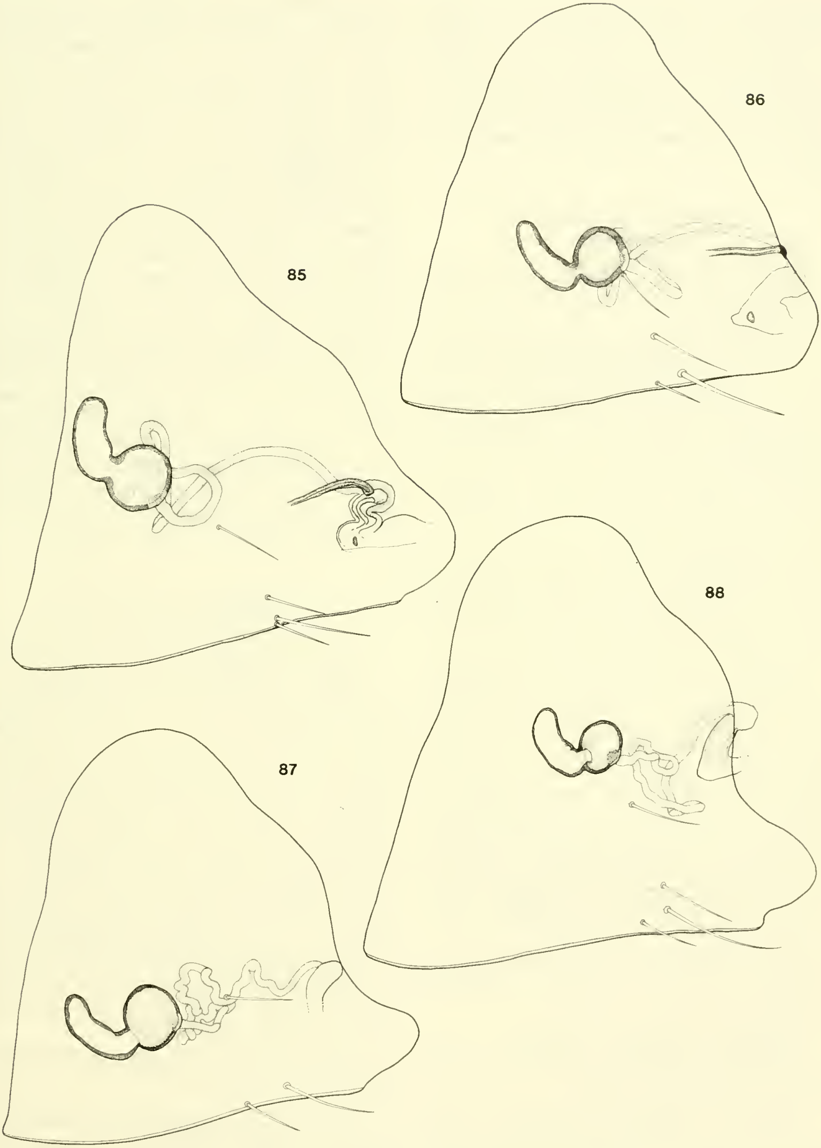
The number and placement of the distal spiniforms were considered to be important by Linsdale and Davis (1956) in distinguishing these two forms. In 73 specimens of *f. congruens* from the type locality, 36 had a full complement (three distal, one proximal on both sides), 19 had one proximal missing on one side, 7 had one proximal moved up near the distal row, and 11 had no proximal spiniforms at all. A series of 17 *f. falsicalifornicus* from Los Angeles had no proximal spiniforms. Of 54 males of *f. falsicalifornicus* examined in the present study, 7 had proximal spiniforms on at least one side and the remainder had none. Of the many *f. congruens* examined, 72 percent had at least one proximal spiniform and 63 percent had proximal spiniforms on both sides. Only an occasional specimen (1 percent) had one or more spiniforms moved up to or near the distal row. The proximal spiniform is evidently in the process of being lost in both forms, but the process has progressed further in *f. falsicalifornicus* than in *f. congruens*. Its presence in some *f. falsicalifornicus* and absence in some *f. congruens* reduces its value as a character.

The fixed process of the clasper is used by Linsdale and Davis (1956) and by Hopkins and Rothschild (1962) to separate *falsicalifornicus* and *congruens*. In material examined in the present study, the general shape was found subject to variation. That of *f. falsicalifornicus* is always longer than broad, and that of *f. congruens* broader than long.

In females, sternum VII varies in contour within populations both in regard to breadth of the ventral lobe and depth of the posterodorsal sinus. The sinus varies from prominent in some specimens to absent in others. The range of variation is completely overlapping between the two subspecies.

The posterior margin of the female tergum VIII has been used to separate species by Hopkins and Rothschild (1962). In *f. falsicalifornicus*, there is considerable variation in its shape. Specimens of *f. congruens* from coastal California may or may not possess a dorsal lobe. Often there is no production of the posterodorsal margin, and rarely does this lobe exceed the ventral production of tergum VIII. Consequently, the sinus between these lobes is either very shallow or absent. Specimens of *f. congruens* from the Sierra Nevada foothills show a definite, broad posterodorsal lobe of tergum VIII which extends beyond the ventral portion of the tergum forming a broad, shallow sinus. Females of *f. falsicalifornicus* from Los Angeles County differ only slightly from coastal *f. congruens* in this respect.

One of the oddities found by the study of many specimens, particularly *f. congruens*,



Figs. 85-88. Female seventh sternum and spermatheca: 85, *A. falsicalifornicus congruens*; 86, *A. falsicalifornicus falsicalifornicus*; 87, *A. walkeri*; 88, *A. martini*.

is that specimens from more humid, coastal areas (e.g., Santa Margarita, San Luis Obispo County) are darker, i.e., more heavily pigmented. This character is also found in the wood rat hosts (Hooper 1938) and is used here as a subspecific character, but it has little value as a taxonomic character in fleas.

Anomiopsyllus falsicalifornicus falsicalifornicus Fox

Figs. 14, 37, 60, 72, 86, 95

Anomiopsyllus californicus: Fox, 1926 (nec Baker, 1904), Pan-Pacific Ent. 2: 183; Wagner, 1930, Mag. Parasitol. Moscow 1: 35.

Anomiopsyllus falsicalifornicus: Fox, 1929, Ent. News 40: 218; Collins 1936, Ent. News 40: 137; Hubbard, 1947, Fleas of western North America: 78-80; Jellison, Locker, and Bacon, 1953, Index to the literature of Siphonaptera of North America, Suppl. 1: 10; Linsdale and Davis, 1956, Univ. Calif. Publ. Zool. 54(5): 306-308; Holland, 1965, Canadian Ent. 97: 1052; Barnes, 1965, Pan-Pacific Ent. 41(4): 278; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Coultrip et al., 1973, J. Med. Ent. 10(3): 306.

Anomiopsyllus falsicalifornicus falsicalifornicus Hopkins, 1952, J. Wash. Acad. Sci. 365; Knudsen, 1956, Bull. South. Calif. Acad. Sci. 55(1): 1-6; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 402-403; Holland, 1965, Canadian Ent. 97: 1053; Lewis 1974, J. Med. Ent. 11(2): 154.

Diagnosis: The males of *A. falsicalifornicus falsicalifornicus* are distinguished from *A. f. congruens* by the shape of the distal arm of sternum IX and the fixed process of the clasper being longer than broad. Sternum IX is two to three times as broad mesally as in *f. congruens* and has the apex gently rounded and equipped at its posterior margin near the apex with one or two stout setae. The movable process is similar to *f. congruens* but lacks the proximal spiniform setae.

Female characters are not sufficiently distinctive to separate subspecies of *falsicalifornicus.*

Type data: That of the species.

Recorded distribution: California: Claremont, Los Angeles County, west to Beverly Glen, Los Angeles County.

Material examined: California: Kern County: 3 males, 4 females, ex *Neotoma lepida*, Poso Creek, 3.5 km S, 8.8 km W of Granite Station, 23 May 1957, (BVC 1781). Los Angeles Co.: 6 females, ex *Neotoma fuscipes*, Sepulveda Canyon, Los Angeles, 11 November 1941, G. Augustson (HF41-148c); 3 males, 7 females, ex *Neotoma fuscipes*, Beverly Glen, June 29, 1941, G. Augustson (HF41-45 GA); 4 females, ex *Neotoma fuscipes*, Los Angeles, 27 April 1941, G. Augustson (HF41-45 GA); 1 female, ex *Neotoma fuscipes*, same locality, 16 November 1940, G. Augustson (HF40-146 GA); 3 males, 3 females, ex *Neotoma fuscipes*, Sepulveda and Mission Roads, 5 May 1959, D. Rohe (BVC 15754); 2 males, 3 females, ex *Neotoma fuscipes*, 4 km N of Bel Air, 17 November 1959, Murray and Rohe (BVC 14703); 17 males, 27 females, ex *Neotoma fuscipes* nests, plus 33 females, 14 males reared from larvae, Sepulveda and Mission Road, 28 March 1962, D. Rohe; 1 male, 4 females, ex *Neotoma fuscipes* nest, Malibu Creek Cornell, 9 May 1961, A. Barnes; 11 males, 19 females, ex *Neotoma fuscipes* nests, San Gabriel Canyon, 13.2 km N of Azusa, 17 December 1956, A. Barnes.

Anomiopsyllus walkeri Barnes

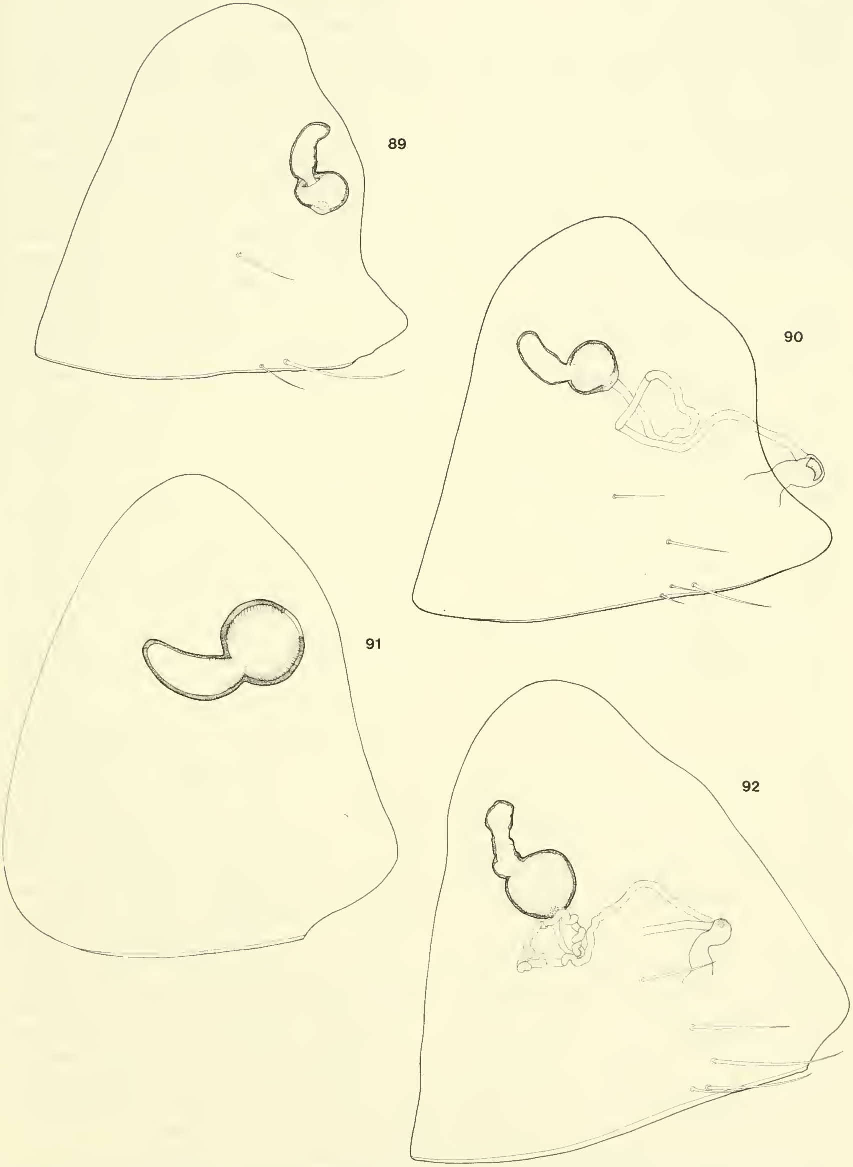
Figs. 13, 38, 59, 74, 87, 94

Anomiopsyllus walkeri Barnes, 1965, Pan-Pacific Ent. 41(4): 272-280; Lewis, 1974, J. Med. Ent. 110: 154.

Diagnosis: Barnes (1965) indicated that *A. walkeri* was related to *A. nudatus*, but may be distinguished on the basis of four spiniforms on the movable process of the clasper with three on the distal portion and one on the proximal portion. Since Holland's description of *A. martini*, it would appear that *walkeri* would be more closely related to *martini* than *nudatus*. The aedeagus of *A. walkeri* differs markedly from *nudatus* in that *walkeri* has a heavily sclerotized dorsal margin and a well-defined dorsomedian "hump" above and slightly anterad to the aedeagal struts. The neck of the aedeagus curves ventrad from the longitudinal axis and the apodeme curves dorsad.

Female characters are not sufficiently distinctive to separate *walkeri* from *nudatus* and *martini*.

Type locality: Male holotype, female allotype from 11 km S, 9 km E of Tehachapi, Kern Co., Calif., ex *Neotoma fuscipes* nest, 19 February 1959 (Barnes). Designated



Figs. 89-92. Female seventh sternum and spermatheca: 89, *A. durangoensis*; 90, *A. novomexicanensis*, 91, *A. traubi* (redrawn from Barrera 1951 and Barnes 1963); 92, *A. oaxacae*.

paratypes: California: Kern Co., 7 males, 19 females, 19 February 1959, 2 females, 2 April 1959; 22 males, 30 females, 22 January 1960; 1 male, 8 females 10 km SE of Tehachapi, 19 February 1959; 7 males, 8 females, 3 km NW of Keene, 18 February 1959; 2 males, 3 females, 3-6 km SW of Glenville, 17 February 1959; 2 males, 1 female, 3 km N, 1 km W of Weldon, 16 March 1960; 5 males, 13 females, 5 km E of Lake Isabella, 18 March 1960. Tulare Co., 2 males, 2 females, 8 km S, 10 km W of Little Lake (Inyo Co.).

Type host: Neotoma fuscipes

Type specimens: The male holotype and female allotype are in the U.S. National Museum. Paratypes are in the following collections: University of California, Berkeley; Bureau of Vector Control, California Department of Public Health, Berkeley, California; British Museum (Natural History), Tring, Hertfordshire; Rocky Mountain Laboratory, Hamilton, Montana; U.S. Public Health Service Field Station, San Francisco, California; private collection of Dr. Robert Traub, Bethesda, Maryland.

Discussion: Barnes (1965) draws attention to the close morphological and distributional relationships between *A. walkeri* and *A. nudatus*, but provides ecological data which supports retention of *walkeri* as a full species.

Anomiopsyllus walkeri replaces *A. nudatus* in the Tehachapi and southern Sierra Nevada Mountains of California. This type of replacement is typical of *Anomiopsyllus* species distribution, with no instance known of two *Anomiopsyllus* species inhabiting the same nest, or even the same wood rat colony.

The area of contact between the two species was examined with this in mind. Special attention was given to the possibility of morphological intergradation and to the habitats in which the two species were found. Substantial numbers of wood rat (*N. fuscipes*) nests were collected from the type locality and adjacent areas during the winter and spring of 1959 and 1960. Fleas were removed from nests by means of a modified Berlese funnel and were examined. Habitat notes were taken along with notes on weather conditions at the time of collection.

The type locality of *A. walkeri* is on the east slope of Double Mountain, the easternmost peak of the Tehachapi chain, and is at 1463 m to 1585 m. The dominant vegetation consists of juniper (*Juniperus occidentalis*) and Joshua tree (*Yucca brevifolia*) woodland, sagebrush (*Artemisia* sp.) and several species of *Eriogonum*. This vegetation characterizes a desert habitat in that area. Such habitats usually have some persistent snow (at least in patches) during midwinter. The average annual rainfall is approximately 30 cm. In the south, alluvial fans slope into Antelope Valley. The plain, which is relatively flat, slopes gradually from about 1067 m in the west to 762 m in the south and east. The valley is largely under cultivation, but on the alluvial fans and in the remaining natural areas on the valley floor juniper-Joshua tree woodland also exists as habitat for *N. fuscipes* along with creosote bush (*Larrea tridentata*), a shrub characteristic of moderate elevation and gentle slopes in the Mojave Desert. Rare winter snows do not persist even for a day in Antelope Valley or on the slopes of Double Mountain below 1220 m. Average annual precipitation is 13 cm at Lancaster and 16 cm at Mojave, two nearby weather stations on the valley floor.

Nest collections were made at and near the type locality on slopes at lower elevations and in Antelope Valley on 19 February 1959; 1-2 April 1959 and on 22 January 1960. A total of 51 nests was collected, with 34 containing fleas, of which 24 contained *Anomiopsyllus* spp., either *walkeri* or *nudatus*. *Anomiopsyllus walkeri* alone was removed from 11 of 22 nests collected at 1402 m or above in juniper-Joshua tree woodland. *Anomiopsyllus nudatus* alone was removed from 13 of 29 nests collected in juniper-Joshua tree-creosote bush at 1280 m or below. A total of 31 male *walkeri* was collected at the higher elevations, and 52 male *nudatus* from the lower. The females were not considered since they are indistinguishable. No evidence of morphological intergradation was found.

It appears that *A. walkeri* is better adapted to areas having some persistent winter snow and higher rainfall. *Anomiopsyllus nudatus* is better adapted to lower elevations characterized by no winter snow, much less rainfall, and the occurrence of creosote bush. In neither case is the rainfall great. It must be pointed out that the rainfall in the habitat of *walkeri* is roughly twice that for the valley below, where *nudatus* occurs.

Competitive exclusion in the zone of contact may occur between *Anomiopsyllus nudatus* and *A. walkeri* in the larval stage, when both species occupy the same nest. Further evidence of this competitive exclusion between *A. nudatus* and *A. walkeri* is noted when analyzing the collection data outside their zone of contact. *A. nudatus* has been collected elsewhere in California from wood rat hosts and nests far above the winter snow line at elevations up to 2287 m, and in areas with average annual precipitation up to 89 cm or more (e.g., Big Bear, California, with a 94 cm annual average). Collections of *nudatus* in the Sawtooth and Liebre Mountains near Sandburg, south of Antelope Valley, and near Desert Springs, San Bernardino County, California, were made in habitats characteristically occupied by *walkeri* in the zone of contact. *Anomiopsyllus nudatus* is never found within the range of *walkeri*.

In view of the morphological differences and the lack of intergradation at a point of close contact, *A. walkeri* must be considered a full species related to *nudatus*. These con-

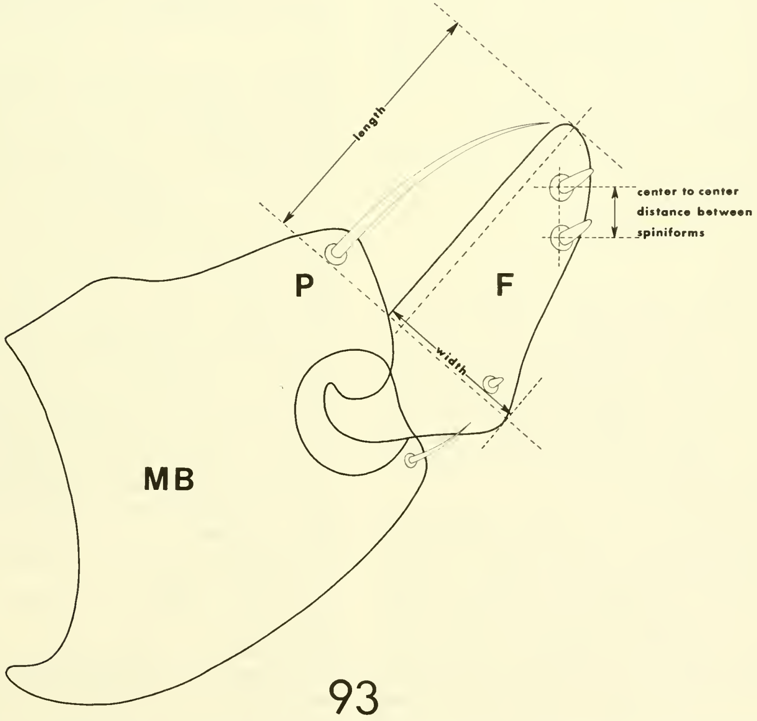


Fig. 93. Diagram of clasper showing measurements used on features of the movable process in the *nudatus* group. All measurements made by means of calibrated eyepiece grid.

siderations further suggest that *walkeri* has evolved in isolation from *nudatus* and has subsequently been brought into contact with the parent species.

Anomiopsyllus martini Holland

Figs. 16, 39, 61, 73, 88, 95

Anomiopsyllus martini Holland, 1965, Canadian Ent. 97: 1054-1056; Tipton and Mendez, 1968, Pacific Insects 10(1): 179; Lewis, 1974, J. Med. Ent. 11(2): 154.

Anomiopsyllus princei Barnes, 1965, Pan-Pacific Ent. 41(4): 276-278 (new synonomy); Haas et al., 1973, J. Med. Ent. 10(3): 282.

Diagnosis: Anomiopsyllus martini has been considered a close relative of *A. nudatus* and *A. walkeri* (Holland 1965, Barnes 1965). The males can be separated by the presence of four spiniforms on the movable process rather than three as in *nudatus* and from *walkeri* by two long, closely placed thick bristles at the arc of curvature of sternum IX. *Anomiopsyllus martini* also differs from *walkeri* in that it has only three heavy setae on the apex of sternum IX, whereas *walkeri* has a fourth smaller seta.

Female characters are not sufficiently distinctive to separate *martini* from *nudatus* and *walkeri*.

Type locality: 16 km W of El Salto, Durango, Mexico, 2744 m.

Type host: Nest of *Sciurus aberti* Woodhouse.

Type specimens: Male holotype and female allotype, 55 male and 59 female paratypes on slides, and 187 male and 207 female paratypes in alcohol collected on 21 June 1964 in a hollow in a dead pine tree; 3 male and 2 female paratypes, same data, but in another tree, on 11 July 1964 by J. E. H. Martin and deposited in the Canadian National Museum.

Discussion: The recorded geographical distribution of this species is limited to two collections: one from El Salto, Durango, Mexico, at an elevation of 2744 m, and one from Catron County near Luna, New Mexico, at an elevation of 2195 m. Both collections were from *Sciurus aberti* and its nest. *Anomiopsyllus martini* and *A. durangoensis* are the only species of the genus, of which we are aware, that are not associated with wood rats.

We list *A. princei* Barnes as a synonym of *A. martini* Holland, even though there are some slight differences in the two populations. In both species there are three distal and one proximal spiniforms on the movable process of the clasper, and the distal arm of sternum IX bears three subapical thick bristles with the posterior margin broadly rounded in the middle.

There are several isolated populations of *S. aberti* squirrels associated with stands of yellow pine in Arizona, New Mexico, and Utah. Further collecting is required to determine if the distribution of *A. martini* is consistent with that of its apparent host, *S. aberti*.

Anomiopsyllus durangoensis Holland

Figs. 26, 47, 63, 75, 89, 95

Anomiopsyllus durangoensis Holland, 1965, Canadian Ent. 97: 1056-1058; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Anomiopsyllus durangoensis is apparently sympatric with *A. martini* but associated with *Peromyscus* sp. Holland (1965) indicated that *A. durangoensis* is closely related to *A. amphibolus* (males) in that both have a triangular-shaped movable process with two spiniforms, but in *durangoensis* both spiniforms are distal. On this basis *durangoensis* would appear to be more closely related to *A. novomexicanensis*, *A. traubi*, and *A. oaxacae*, which possess only distal spiniforms, whereas *A. amphibolus* also possesses one proximal and one distal spiniform. The distal arm of sternum IX is truncate to subtruncate and bears three short, heavy apical setae; the remaining ventral two-thirds bears fewer and thinner setae than in *martini* and *A. n. hiemalis*.

Female characters are not sufficiently distinctive to separate *durangoensis* from *martini* or *n. hiemalis*.

Type locality: 5 km W of Durango, Durango, Mexico, 1982 m.

Type host: Mouse nest (possibly *Peromyscus* sp.)

Type specimens: Male holotype and female allotype, 11 male and 12 female paratypes collected on 24 June 1964 in a nest in a yucca plant by J. E. H. Martin and deposited in Canadian National Museum.

Discussion: The known geographical dis-

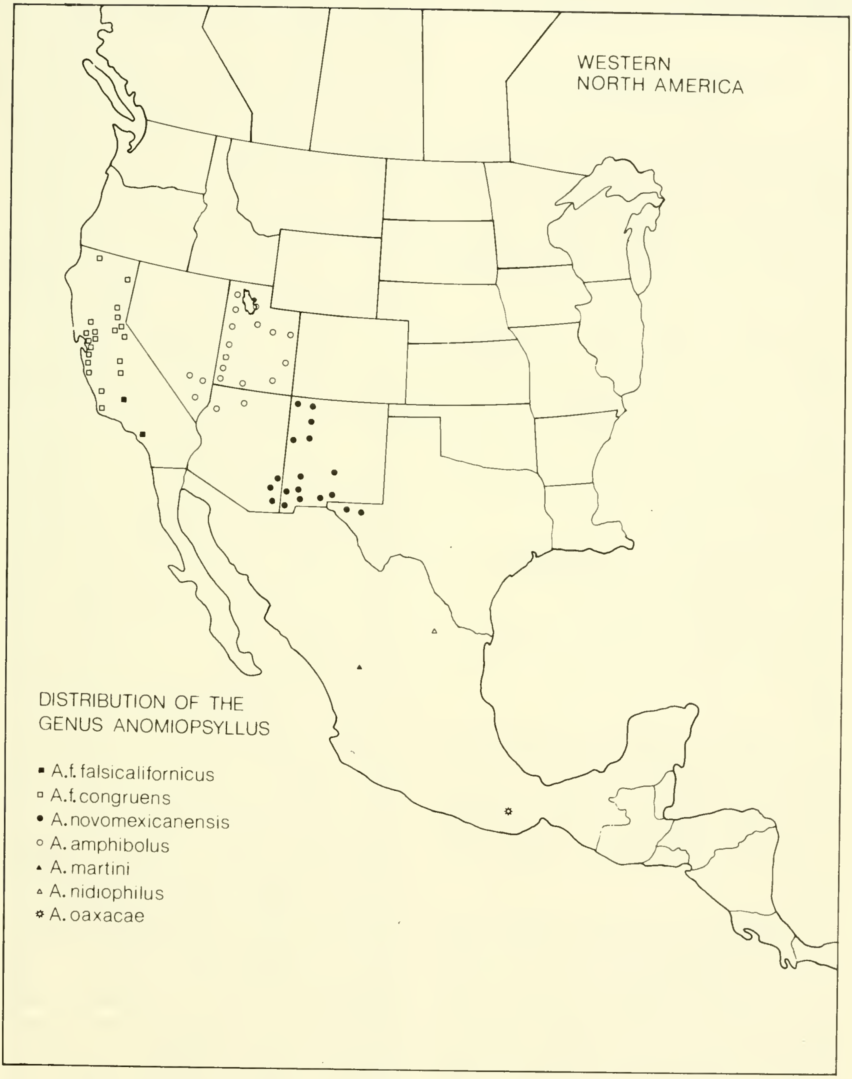

WESTERN
NORTH AMERICA
DISTRIBUTION OF THE
GENUS ANOMIOPSYLLUS
■ A.f. falsicalifornicus
□ A.f. congruens
● A. novomexicanensis
○ A. amphibolus
▲ A. martini
△ A. nidiophilus
✡ A. oaxacae

Fig. 94. Map showing the distribution of *Anomiopsyllus* species.

tribution is limited to the type locality near Durango, Durango, Mexico. Intensive collecting in Arizona and New Mexico may reveal the presence of *A. durangoensis*.

Anomiopsyllus novomexicanensis Williams and Hoff

Figs. 27, 49, 62, 76, 90, 95

Anomiopsyllus novomexicanensis Williams and Hoff, 1951, Proc. U.S. Nat. Mus. 101(3278): 307-309; Traub and Hoff, 1951, Amer. Mus. Nov. 1530: 3-4; Vargas, 1960, Med. Rev. Mexicana 40(849): 4; Holland 1965, Canadian Ent. 97: 1053; Jellison and Glesne, 1967, Index to the literature of Siphonaptera of North America, Suppl. 2: 13-19; Rail et al., 1969, J. Med. Ent. 6(1): 93; Miller et al., 1970, J. Med. Ent. 7(6): 698; Graves et al., 1974, J. Med. Ent. 11(4): 490-497.

Diagnosis: Anomiopsyllus novomexicanensis, though similar in many taxonomic characters to the *nudatus* group, is placed with *A. traubi* and *A. oaxacae* on the basis of having only distal spiniforms. *Anomiopsyllus novomexicanensis* males can be distinguished from other *Anomiopsyllus* species by the loss of the long bristle on the fixed process of the clasper.

Females are readily identified from other *Anomiopsyllus* species by the presence of a prominent comma-shaped sclerotization in a portion of the bursa copulatrix.

Type locality: 9.7 km E of Albuquerque, Bernalillo County, New Mexico.

Type host: Neotoma micropus canescens Allen.

Type specimens: Male holotype and female allotype, 332 male and 605 female paratypes collected on 10 October 1948; 62 male and 126 female paratypes on 28 February 1948; 16 male and 4 female paratypes in December 1947 by L. A. Williams and C. C. Hoff, deposited in U.S. National Museum.

Material examined: Arizona: Cochise Co.: 1 male, 1 female, ex *Neotoma lepida*, 19 km W of Bowie on Tucson Rd., 914 m (cactus), 11 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 8 km SW of San Simon, 914 m (cactus), 13 October 1938 (PHS); 1 male, ex *Neotoma lepida*, 9 km S of Bowie, 974 m (cactus), 15 October 1938 (PHS). Graham Co.: 3 males, 3 females, ex *Neotoma lepida*, 32 km NW of Duncan, 1128 m (grass), 28 February 1939 (PHS); 1 male, ex *Neotoma lepida*, 32 km E of Safford, 975 m (cactus), 5 October 1938; 1 male, ex *Neotoma lepida*, 24 km S of Safford on Bowie Rd., 1113 m (cactus), 6 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 38 km NW of Duncan, 1128 m (grass), 1 March 1939 (PHS); 2 females, ex *Neotoma lepida*, 24 km E of Safford, 1067 m (grass), 4 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 40 km S of Safford on Bowie Rd., 1128 m (cactus), 8 October 1938 (PHS); 1 female, ex *Neotoma lepida*, 45 km NW of Duncan, 1128 m (grass), 2 March 1939 (PHS). Greenlee Co.: 3 males, ex *Neotoma lepida*, 6 km SE of Duncan, 1097 m (grass), 4 March 1939 (PHS); 1 male, ex *Neotoma lepida*, 13 km SE of Duncan at N. Mexico line, 1113 m (grass), 6 March 1939 (PHS); 1 male, 1 female, host unknown (*Onychomys leucogaster capitulatus*?), no locality, 2 December 1938 (PHS). *New Mexico:* Bernalillo Co.: 1 female, ex *Neotoma micropus*, 10 October 1948, L. Williams (RM); 3 males, 3 females, ex *Neotoma albigula*, 24 km W of Albuquerque, (juniper, cactus—range), 16 May 1939 (PHS); 4 males, 4 females, ex *Neotoma* sp., 10 October 1948, L. Williams (RM); 24 males, 1 female, ex *Neotoma canescens*, Albuquerque, 10 October 1948, Williams and Hoff; 1 male, 1 female, ex *Neotoma canescens*, Albuquerque, 28 February 1948, Williams and Hoff. Dona Ana Co.: 2 males, 2 females, ex *Neotoma albigula*, 16 km W of Las Cruces, 1097 m (cactus, mesquite—desert), 15 April 1939 (PHS); 3 males, 3 females, ex *Neotoma albigula*, 11-16 km W of Hatch, 1280 m (yucca, grass), 12 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 8-11 km S of Hatch, 1280 m (chaparral), 10 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 3-6 km S of Salem, 1280 m (mesquite), 11 May 1939 (PHS); 1 female, ex *Neotoma albigula*, Las Cruces, February 1939 (PHS); 1 female, ex *Onychomys leucogaster*, 11-16 km W of Hatch, 1280 m (grass), 12 May 1939 (PHS); 1 female, ex *Dipodomys ordii*, 16 km W of Las Cruces, 1097 m (cactus—desert), 15 April 1939 (PHS). Grant Co.: 3 females, ex *Neotoma albigula*, 19 km NE of Lordsburg, 1372 m (cactus, mesquite), 12 April 1939 (PHS). Hidalgo Co.: 1 male, 4 females, ex *Neotoma albigula*, 19-22 km

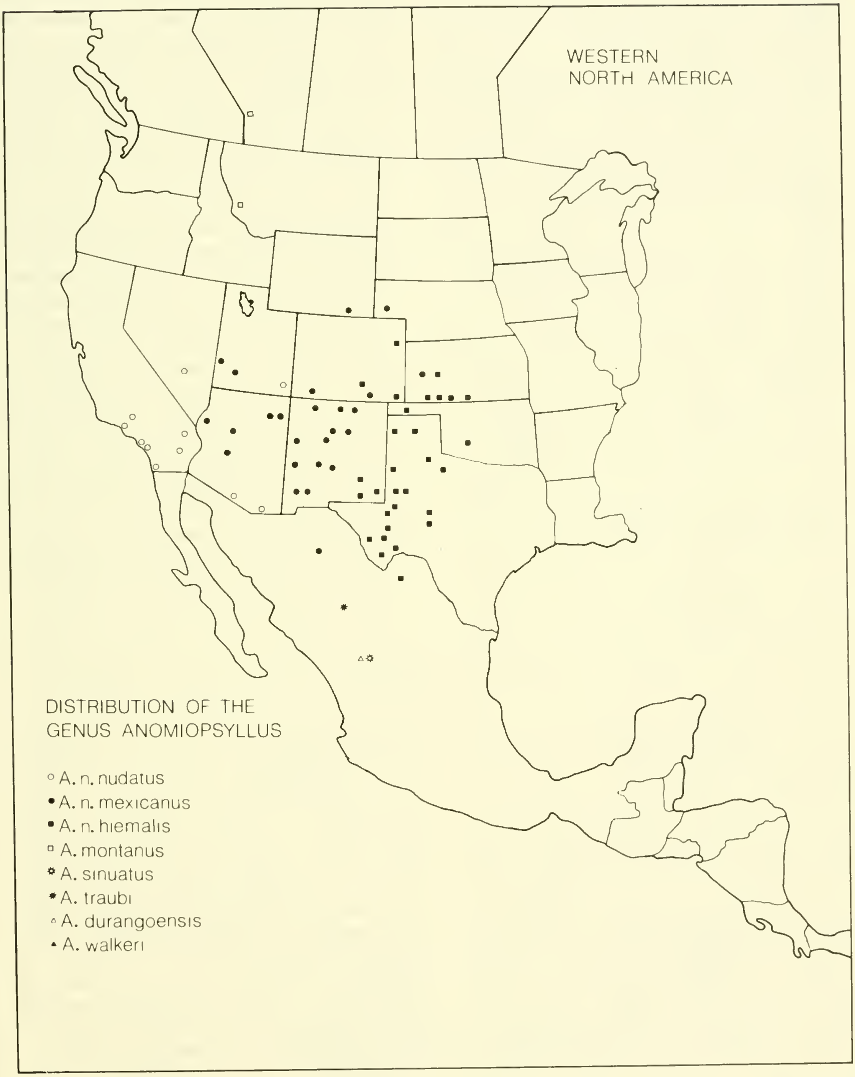

WESTERN
NORTH AMERICA
DISTRIBUTION OF THE
GENUS ANOMIOPSYLLUS
○ A. n. nudatus
● A. n. mexicanus
■ A. n. hiemalis
□ A. montanus
✲ A. sinuatus
✱ A. traubi
△ A. durangoensis
▲ A. walkeri

Fig. 95. Map showing the distribution of *Anomiopsyllus* species.

NW of Lordsburg, 1292 m (cactus), 11 April 1939 (PHS); 2 females, ex *Neotoma albigula*, 4.8 km S of Lordsburg, 1292 m (brush), 14 April 1939 (PHS); 5 males, 5 females, ex *Neotoma* sp., 23 km NW of Lordsburg, 1292 m (mesquite), 8 April 1939 (PHS); 1 male, 1 female, ex *Neotoma lepida*, 21 km N of Rodeo, 1341 m (cactus), 20 October 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida*, 32 km N of Rodeo, 1402 m (cactus), 21 October 1938 (PHS); 2 males, 2 females, ex *Neotoma lepida* nest, 8 km N of Rodeo, 1341 m (cactus), October 1938 (PHS); 1 female, ex *Peromyscus maniculatus*, 32 km N of Rodeo, 1402, (grass, cactus), 21 October 1938 (PHS). Lincoln Co.: 1 male, 2 females, ex *Neotoma albigula*, 6 km NE of Carrizozo, 1646 m (yucca), 15 April 1949 (PHS). Luna Co.: 2 males, 5 females, ex *Neotoma albigula*, 5 km E of Deming, 1372 m (chaparral), 2 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 5-8 km S of Deming, 1372 m (chaparral), 5 May 1939 (PHS); 1 female, ex *Dipodomys ordii*, 5-8 km N of Deming, 1372 m (yucca, mesquite), 6 May 1939 (PHS). Otero Co.: 1 male, 1 female, ex *Neotoma albigula*, 10 km E of La Luz, Lincoln Nat. Forest, 1372 m, 22 March 1949 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 11 km NE of La Luz, Lincoln Nat. Forest, 1463 m, 24 April 1949 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 4 km E of Tularosa, 1524 m, 25 March 1949 (PHS). Rio Arriba Co.: 1 female, ex *Neotoma albigula*, 3 km SW of Espanola, 1982 m (grass, sage, cactus), 30 May 1939 (PHS). Sandoval Co.: 2 males, 3 females, ex *Neotoma mexicana*, 3 km E of Bernalillo, 1524 m (juniper, sagebrush), 23 July 1949 (PHS); 1 male, 4 females, ex *Neotoma albigula*, 8 km NW of Bernalillo, 1585 m (sage, juniper), 18 May 1939 (PHS). San Juan Co.: 1 male, 1 female, ex *Neotoma albigula*, 8 km SE of Aztec, 2134 m (juniper), 28 May 1949 (PHS). Sierra Co.: 1 male, 1 female, ex *Neotoma albigula*, 32 km N of Engle, 1280 m, 24 March 1949 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 13 km E of Hot Springs, 1280 m, 25 March 1949 (PHS); 1 male, 3 females, ex *Neotoma albigula*, 19 km S of Hot Springs, 1220 m (cactus, sage—desert), 19 April 1939 (PHS); 1 female, ex *Neotoma albigula*, 8-10 km S of Hillsboro, 1555 m (sage, mesquite—plateau), 28 June 1939 (PHS). Socorro Co.: 4 males, 7 females, ex *Neotoma albigula*, 5 km N of Bernardo, 1433 m (grass, sage, mesquite—range), 12 May 1939 (PHS); 4 males, 4 females, ex *Neotoma albigula*, Abo-Pass, 10 km W of Schoole, 1738 m (grass, oaks, juniper), 11 May 1939 (PHS); 2 males, 2 females, ex *Neotoma albigula*, 3 km SW of San Antonio (range), 6 May 1939 (PHS); 1 male, 4 females, ex *Neotoma albigula*, 3 km N of Escondida, 1433 m (near irrigated crops—gravel banks), 2 May 1939 (PHS); 1 male, 1 female, ex *Neotoma albigula*, 16 km W of Socorro, 1524 m (grass, sage—range), 4 May 1939 (PHS); 1 male, 5 females, ex *Neotoma albigula*, 16 km E of San Antonio, 1372 m (sage, cactus—range), 5 May 1939 (PHS); 2 females, ex *Neotoma albigula*, 7 km N of Polradera, 1463 m (sage, mesquite), 3 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 12 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 3 km W of Socorro, 1402 m (cactus, mesquite—range) 2 May 1939 (PHS). Valencia Co.: 4 males, 5 females, ex *Dipodomys merriami*, 3 km W of Belen, 1463 m (grass, sage—dump grounds), 9 May 1939 (PHS); 1 female, ex *Neotoma albigula*, same locality, 1463 m (grass, sage—dump grounds), 9 May 1939 (PHS); 2 females, ex *Neotoma albigula*, 13 km W of Belen, 1524 m (juniper, sage—range), 9 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 31 km W of Hoshunas, 1494 m (sage—range), 10 May 1939 (PHS); 1 female, ex *Neotoma albigula*, 24 km S of Correo, 1524 m (sage, juniper), 25 April 1939 (PHS); 1 male, ex *Peromyscus truei*, 12.9 km W of Belen, 1524 m (juniper—range), 9 May 1939 (PHS); 1 male, ex *Peromyscus boylei*, Harrington Ranch, 1524 m (sage, juniper), 26 April 1939 (PHS). *Texas:* Hudspeth Co.: 1 female, ex *Neotoma*, 19 September 1940 (RM); 3 males, 1 female, ex *Neotoma* nest, Allamore, 19 September 1940 (RM). Culberson Co.: 2 males, 2 females, ex *Neotoma albigula*, 31 March 1942 (PHS).

Discussion: In their remarks following the description of *A. novomexicanensis* Williams and Hoff (1951) grouped this species with *A. n. hiemalis* on the basis of its having three spiniforms on the movable process. They considered the genus to contain two species groups: those with two such spiniforms (i.e., *A. amphibolus*) and those with three (i.e., *nudatus hiemalis*). *Anomiopsyllus falsicalifornicus* with four (usually) was not mentioned.

Characteristics of the fixed process included in the diagnosis are not found in *Anomiopsyllus* species and would apparently place *A. novomexicanensis* in a monotypic species group. The shape, articulation, and adornment of the movable process in *novomexicanensis* would seem to indicate its closeness to *A. traubi* and probably place it in the group which includes *A. traubi* and *A. oaxacae.*

Hosts: Anomiopsyllus novomexicanensis has been collected from four wood rat hosts: *Neotoma albigula, N. micropus* (type host), *N. mexicana*, and *N. lepida stephensi.* Occasional hosts include *Peromyscus, Dipodomys*, and a few sciurids with about the same infestation rate as for other *Anomiopsyllus* species. There were 52 wood rat collections in the material examined, of which *N. albigula* predominated (33), followed by *N. lepida stephensi* (15), *N. micropus* (4), and *N. mexicana* (1). The known range of *A. novomexicanensis* falls within the distribution of *N. albigula* and *N. mexicana*, but occupies only a small portion of either. The collection records for *N. lepida* are all from eastern Arizona. The distribution of *N. micropus* does not extend west beyond New Mexico (Hall and Kelson 1959). As is undoubtedly the case with other *Anomiopsyllus* species for which considerable data exist, the distribution of *A. novomexicanensis* is limited by factors other than that of host distribution.

Distribution and habitat (Fig. 95): The known distribution of *A. novomexicanensis* includes most of southern and central New Mexico, a small portion of southeastern Arizona (Greenlee and Graham counties) and the westernmost corner of Texas (Culberson and Hudspeth counties). To the north and west its distribution interdigitates with that of *A. nudatus mexicanus* and to the east (Texas) with *A. nudatus hiemalis.*

Collection records, where habitat clues and elevations are given, show that *A. novomexicanensis* is a flea of the Chihuahuan

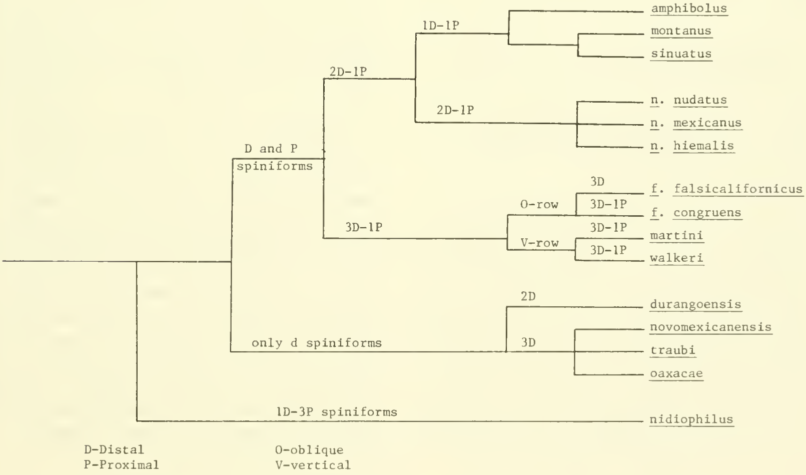

amphibolus
1D-1P
montanus
sinuatus
2D-1P
n. nudatus
2D-1P
n. mexicanus
D and P
spiniforms
n. hiemalis
3D
f. falsicalifornicus
0-row
3D-1P
f. congruens
3D-1P
3D-1P
martini
V-row
3D-1P
walkeri
2D
durangoensis
novomexicanensis
only d spiniforms
3D
traubi
oaxacae
1D-3P spiniforms
nidiophilus
D-Distal
P-Proximal
0-oblique
V-vertical

Diagram 1. Cladogram illustrating the relationships of species and subspecies in the genus *Anomiopsyllus*, based on the spiniforms of the movable process on the clasper.

biotic province. It occupies the desert plains and the arid grassland-mesquite belt mentioned by Bradt (1932) and Benson (1933). It also inhabits the low wastelands where its hosts occur, but it primarily occupies the Chihuahuan roughlands belt of Blair (1940) and the lowest edges of the pinyon-juniper belt (sabinal belt of Dice 1942) at elevations of 1220 to 1524 m. Extreme southern New Mexico in Luna, Dona Ana, and Otero counties, where *novomexicanensis* is the only *Anomiopsyllus* recorded, also falls within the Chihuahuan province (Dice 1943). Elements of the Chihuahuan desert interdigitated with portions of the Colorado plateau to the north (Dice 1943, Fenneman 1931). Here, *A. novomexicanensis* is found at lower elevations and *A. n. mexicanus* at higher elevations. Of 52 collections of *novomexicanensis*, 94 percent were made below 1577 m ($\bar{x} = 1357$ m), but 83 percent of the *A. n. mexicanus* collections were made above 1524 m and 72 percent above 1692 m ($\bar{x} = 1829$ m).

Further evidence that *novomexicanensis* occurs primarily in the lower desert habitats is offered by clues to vegetation type in Public Health Service collection records. These records, where available, have been included in the collection data under material examined. References to cactus, yucca, and mesquite are much more common to the Chihuahuan province where *novomexicanensis* occurs, and references to pinyon, juniper, and sagebrush are much more common to the Colorado Plateau where *A. n. mexicanus* occurs.

Differences in habitat occupied by the two species are probably dependent on two factors: (1) climate, particularly humidity or available moisture as in the observed habitat division between *A. falsicalifornicus* and *A. nudatus nudatus* or between *n. nudatus* and *walkeri*, and (2) competitive exclusion resulting from two related species utilizing the same host niche. Altitudinal overlap in the records shown here may be explained on the basis of differences in microclimate brought about by slope exposure, rain shadow, and precipitation pattern.

Anomiopsyllus traubi Barrera

Figs. 28[6], 48[6], 91[6], 94

Anomiopsyllus traubi Barrera, 1951, Ciencia, 12(6-9): 197; Vargas, 1960, Med. Rev. Mexicana, 40(849): 1-4; Hopkins and Rothschild, 1962, Catalogue of the Rothschild Collection of Fleas III: 401-402; Holland, 1965, Canadian Ent. 97: 1054; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: A. traubi males can be distinguished from *A. novomexicanensis* and *A. oaxacae* in that the distal arm of sternum IX has 5-7 stout apical setae. The posterior margin of sternum IX is bare except for a subbasal row of 5-7 long, stout bristles intermixed with long, slender bristles and a single submedian seta. The movable process is broadly triangular and rounded at the posteroventral angle containing a row of three spiniforms placed vertically along the posterior margin.

Type locality: Cueve de Belen, near Zimapan, Hidalgo, Mexico.

Type host: Nest of rodent.

Type specimen: Male holotype collected on 2 November 1950 by A. Barrera, deposited in Alfredo Barrera's collection.

Discussion: Barnes (1963) examined only two male paratypes of this species: one provided by William L. Jellison and one provided by Robert Traub. These specimens had been mounted in Hoyer's mounting medium, and the exoskeletons were fractured by shrinkage of the medium, resulting in the destruction of a number of characters of taxonomic value, particularly in the aedeagus. Hopkins and Rothschild (1962) believe *A. traubi* to be most closely related to *A. novomexicanensis*, but the fixed process of *A. novomexicanensis* is unique in the genus whereas that of *traubi* is most like *A. oaxacae*. The distal arm of sternum IX in *traubi* and *oaxacae* differ by virtue of the subbasal angle of the posterior margin of this structure. The true relationships of *traubi* and *oaxacae* will remain uncertain until additional specimens are available.

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[6] Figures 28, 48, and 91 were redrawn from Barrera (1951) and Barnes (1963). The aedeagus and sternum VIII of the male were not illustrated because of the lack of a specimen.

Anomiopsyllus oaxacae Barnes

Figs. 29, 50, 64, 77, 92, 95

Anomiopsyllus oaxacae Barnes, 1965, Pan-Pacific Ent. 41(4): 278-279; Lewis, 1974, J. Med. Ent. 11(2): 154.

Diagnosis: Barnes (1965) indicated that *A. oaxacae* is most closely related to *A. f. falsicalifornicus* but very different from that species and all other species of *Anomiopsyllus* in that it possesses more and generally longer bristles. *Anomiopsyllus oaxacae* is probably closer to *A. traubi* than to *f. falsicalifornicus*, based on the presence of only distal spiniforms on the movable process in *A. traubi*, whereas *f. congruens* still retains a proximal spiniform. The movable process is broad almost to the point of being rectangular in shape and is equipped with three mesad spiniform setae parallel to the posterior margin of the process. The proximal arm of sternum IX is similar to that of *f. falsicalifornicus*, but the distal arm is long, narrow, and almost parallel sided and armed apically with two posterad rows of heavy, spikelike setae. The posterior margin of the distal arm has a row of 20 evenly spaced, long, thin bristles extending from the base of the lowest apical seta to three-fourths of the distance of the arm. The aedeagal hood extends anterad far beyond the aedeagal struts, and the length of the hood is about equal to the length of the apodeme beyond the anterior margin of the hood.

Length: 1.7 mm.

Type locality: 3 km SE of Matatlàn, Oaxaca, Mexico

Type host: Baiomys musculus (Merriam)

Type specimen: Male holotype collected on 24 July 1953 by R. H. Baker, deposited in U.S. National Museum.

Discussion: This species was described from a single male specimen that was loaned to the senior author by Traub and was originally noted as new by Traub. This specimen represents the southernmost record for the genus. Thus, the range of *Anomiopsyllus* extends into tropical America from whence it reaches northward to Banff, Alberta, Canada. Although *Baiomys musculus* is the type host, the normal host is probably *Neotoma mexicana*, the distribution of which includes Oaxaca, Mexico.

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART IV[1]

Stephen L. Wood[2]

ABSTRACT.— New synonymy is proposed as follows: *Pityophthorus* Eichhoff (= *Pityophthoroides* Blackman), *Scolytodes* Ferrari (= *Ctenophorus* Chapuis), *Araptus pallidus* (Blackman), n. comb. (? = *Neodryocoetes portoricensis* Schedl, *Neodryocoetes devius* Schedl), *Corthylus letzneri* (Ferrari) (= *Corthylus strigilatus* Eggers, *Corthylus columbianus* Schedl, *Corthylus ater* Schedl), *Corthylus spinifer* Schwarz (= *Corthylus guayanensis* Eggers), *Hypothenemus brunneus* (Hopkins) (= *Hypothenemus cryphalomorphus* Schedl, *Stephanoderes bituberculatus* Eggers), *Monarthrum parvum* (Eggers) (= *Monarthrum praeclarum* Wood), *Phloeoborus punctatorugosus* Chapuis (= *Phloeoborus breviusculus* Chapuis), *Phloeotribus pilula* Erichson (= *Phloeotribus australis* Schedl), *Phloeotribus setulosus* Eichhoff (*Phloeotribus dubius* Eichhoff, *Phloeotribus spinipennis* Eggers), *Pityophthorus, pulicarius* (Zimmermann) (= *Pityophthorus cubensis* Schedl), *Pityophthorus subsimilis* Schedl (= *Pityophthorus subimpressus* Bright), *Premnobius cavipennis* Eichhoff (= *Premnobius latior* Eggers), *Scolytus propiguus* Blandford (= *Scolytus penicillus* Schedl), *Xyleborus dryographus* (Ratzeburg) (= *Xyleborus linearis* Schedl), *Xyleborus horridus* Eichhoff (= *Xyleborus flohri* Schedl). *Xyleborus tonsus* (Hagedorn), n. comb., was transferred to *Xyleborus* from *Dryocoetes*. *Pityophthorus aquilus* Blackman and *Pityophthorus cascoensis* Blackman, n. status, were removed from synonymy. *Scolytodes chapuisi*, n. n., is proposed for *Scolytodes* (= *Ctenophorus*) *laevigatus* Chapuis, 1869 (nec Ferrari 1867). The following species are named as new to science: *Araptus crassus* (Panama), *A. obesus* (Brazil), *Cnesinus prominulus* (Mexico), *Conophthorus conicolens* (Mexico), *Microcorthylus vicinus* (Mexico), *Pityophthorus alnicolens* (Mexico), *P. assitus* (Mexico), *P. concinnus* (Mexico), *P. indigens* (Colorado), *P. leechi* (California), *P. solatus* (Mexico), *P. speciosus* (Mexico), *Pseudopityophthorus denticulus* (Texas), *Pseudothysanoes securus* (Mexico), *P. turnbowi* (Texas), *Pycnarthrum fulgidum* (Colombia), *Scolytodes fulmineus* (Venezuela), S. *radiatus* (Costa Rica), *Xyleborinus tribuloides* (Mexico), *Xyleborus devexus* (Florida, Puerto Rico), and *X. laticeps* (Venezuela).

On the following pages several newly discovered cases of synonymy and of species new to science are presented for American Scolytidae. The 21 species new to science represent the genera *Cnesinus* (1), *Pycnarthrum* (1), *Scolytodes* (2), *Pseudothysanoes* (2), *Xyleborus* (2), *Xyleborinus* (1), *Pseudopityophthorus* (1), *Araptus* (2), *Microcorthylus* (1), *Conophthorus* (1), and *Pityophthorus* (7), and they are from the following countries: United States (5, including one which also occurs in Puerto Rico), Mexico (10), Costa Rica (1), Panama (1), Columbia (1), Venezuela (2), and Brazil (1).

NEW SYNONYMY

Pityophthorus Eichhoff

Pityophthorus Eichhoff, 1864, Berliner Ent. Zeitschr. 8:39 (Type-species: *Bostrichus lichtensteini* Ratzeburg, subsequent designation by Hopkins, 1914, Proc. U. S. Nat. Mus. 48:127).

Pityophthoroides Blackman, 1942, Proc. U.S. Nat. Mus. 92:199 (Type-species: *Pityophthoroides pudens* Blackman, original designation). *New synonymy*

In a review of the North and Central American *Pityophthorus* and allied genera, Blackman's *Pityophthoroides pudens* was placed in the genus *Pityophthorus* following a study of the type series. The characters on which *Pityophthoroides* was based intergrade completely with those of *Pityophthorus*. Blackman's name, therefore, must be placed in synonymy.

Scolytodes Ferrari

Scolytodes Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 77 (Type-species: *Scolytodes laevigatus* Ferrari, Monobasic)

Ctenophorus Chapuis, 1869, Synopsis des Scolytides, p. 49 (Type-species: *Ctenophorus laevigatus* Chapuis, monobasic). *New synonymy*

Each type series of *Scolytodes laevigatus* Ferrari and *Ctenophorus laevigatus* Chapuis consists of two males, all four of which were examined. It is clear that they are congeneric, but that they represent different species. Since this generic synonymy creates homonymy, Chapius's species is renamed below.

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Araptus pallidus (Blackman), n. comb.

Neodryocoetes pallidus Blackman, 1942, Proc. U.S. Nat. Mus. 92(3147):103 (Holotype, male; Cayamas, Cuba; U.S. Nat. Mus.)

Neodryocoetes portoricensis Schedl, 1951, Dusenia 2:109 (Holotype, male; Portorico; Schedl Coll). *Probable synonymy*

Neodryocoetes devius Schedl, 1972, Koleopt. Rundschau 50:61 (Holotype, male; Valle Ancón, Pinar del Río, Cuba; Schedl Coll.). *Probable synonymy*

The male holotypes of *Neodryocoetes pallidus* Blackman, *portoricensis* Schedl, and *devius* Schedl were all examined at different times and compared to my series of closely allied *Araptus tenellus* (Schedl). All are 1.7 mm in length, of pale color, and fit the same descriptive notes. Although they have not been compared directly to authentic material, there is a strong possibility of synonymy.

Corthylus letzneri (Ferrari)

Pseudocorthylus letzneri Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 59 (Syntype, male; Venezuela, apparently from Colonia Tovar; Vienna Museum).

Corthylus strigilatus Eggers, 1933, Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat., Paris, Mem. 1:20 (Holotype, male; Colonia Tovar, Venezuela; Paris Mus.). *New synonymy*

Corthylus columbianus Schedl, 1950 (nec. Hopkins, 1894), Dusenia 1:158 (Holotype, female; Comatán, Colombia; Schedl Coll.). *New synonymy*

Corthylus ater Schedl, 1952, Dusenia 3:345 (Replacement name for *columbianus* Schedl). *New synonymy*

A male syntype of *Pseudocorthylus letzneri* Ferrari, the male holotype of *Corthylus strigilatus* Eggers, and the female holotype of *Corthylus columbianus* Schedl were all compared directly to my series from Merida and Rancho Grande (Aragua), Venezuela. All clearly represent the same species.

Corthylus spinifer Schwarz

Corthylus spinifer Schwarz, 1891, Proc. Ent. Soc. Washington 2:114 (Syntypes, females; Key West, Florida; U.S. Nat. Mus.)

Corthylus guayanensis Eggers, 1933, Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat. Paris, Mem. 1:22 (Syntype, male; Camopi, Franz. Guayana; Paris Mus.). *New synonymy*

The male type and female cotype of *Corthylus guayanensis* Eggers from Camopi were compared to my series from Florida, Central America, and Venezuela, some of which were compared to the syntypes of *spinifer* Schwarz. All represent the same common species.

Hypothenemus brunneus (Hopkins)

Stephanoderes brunneus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:31 (Holotype, female; Brownsville, Texas; U.S. Nat. Mus.).

Hypothenemus cryphalomorphus Schedl, 1939, Proc. Roy. Ent. Soc. London 8(1):14 (Holotype, female; Trinidad, British West Indies; British Mus. Nat. Hist.). *New synonymy*

Stephanoderes bituberculatus Eggers, 1940, Arb. Morph. Taxon. Ent. Berlin 7:126 (Holotype, female; Env. de Trois-Rivières, Guadeloupe; Paris Mus.). *New synonymy*

The female holotypes of *Stephanoderes brunneus* Hopkins, *Hypothenemus cryphalomorphus* Schedl, and *Stephanoderes bituberculatus* Eggers were compared directly to my long series from Florida, Texas, and Mexico. Since only one species is represented, the names *cryphalomorphus* and *bituberculatus* must be placed in synonymy.

Monarthrum parvum (Eggers)

Anchonocerus parvus Eggers, 1933, Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat., Paris Mem. 1:22 (Holotype, male; Nouveau Chantier, Guyane Française; Paris Mus.)

Monarthrum praeclarum Wood, 1968, Great Basin Nat. 28:6 (Holotype, male; Manaka, British Guiana; British Mus. Nat. Hist.). *New synonymy*

Because my concept of *Anchonocerus* was quite different from that of Eggers, I overlooked the possibility that any of his species in that genus might be allied to my *Monarthrum praeclarum*. The male holotype of *parvus* was directly compared to my male paratype of *praeclarum*. They are identical.

Phloeoborus punctatorugosus Chapuis

Phloeoborus punctatorugosus Chapuis, 1869, Synopsis des Scolytides, p. 14 (Holotype, male Nouvelle Grenade; Mus. Roy. Nat. Belge)

Phloeoborus breviusculus Chapuis, 1869, Synopsis des Scolytides, p. 14 (Holotype, male; Cayenne; Brussels Mus.). *New synonymy*

The male holotypes of *Phloeoborus punctatorugosus* Chapuis and *breviusculus* Chapuis were directly compared to my series. Except for size they are identical. The name *punctatorugosus* is more widely known in the literature and is retained for this species.

Phloeotribus pilula Erichson

Phloeotribus pilula Erichson, 1847, Archiv Naturgesch. 13(1):138 (Lectotype, male; Peru; Zool. Mus. Berlin, designated by Wood, 1973, Great Basin Nat. 33:181)

Phloeotribus australis Schedl, 1953, Mem. Queensland Mus. 13:80 (Holotype, male; Queensland, Australia; Schedl Coll.). *New synonymy*

Phloeotribus australis Schedl is based on a unique male that is labeled "Queensland." Since this is the only reported member of this genus from Australia, and because the original description and accompanying illustration suggest a South American and not an oriental affinity, the type of this species was of unusual interest from zoogeographical and phylogenetic points of view. The holotype is identical in every respect to specimens compared by me to the lectotype of *pilula* Erichson. This species is widely distributed in Central and South America in *Brosmium*. The Schedl specimen was apparently intercepted in Australia or was mislabeled.

Phloeotribus setulosus Eichhoff

Phloeotribus setulosus Eichhoff, 1868, Berliner Ent. Zeitschr. 12:149 (Lectotype, male; Colombia; Brussels Mus., designated by Wood, 1973, Great Basin Nat. 33:182)

Phloeotribus dubuis Eichhoff, 1868, Berliner Ent. Zeitschr. 12:150 (Holotype?, male; Columbie; Berlin Mus.). *New synonymy*

Phloeotribus spinipennis Eggers, 1930, Ent. Blätt. 26:168 (Holotype, male; Columbie, Moritz; Berlin Mus.). *New synonymy*

The male holotypes of *Phloeotribus dubuis* Eichhoff and *spinipennis* Eggers were compared directly to one another and to my material that had previously been compared to the lectotype of *setulosus* Eichhoff. Except for the pale, callow color of the type of *dubuis*, they are identical. For this reason the names *dubuis* and *spinipennis* must be placed in synonymy.

Pityophthorus aquilus Blackman, n. status

Pityophthorus aquilus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:33 (Holotype, female; Kaibab National Forest, Arizona; U.S. Nat. Mus.)

Bright (1977, Canadian Ent. 109:514) placed in synonymy under *Pityophthorus carinulatus* Swaine, 1925, the names *aquilus* Blackman, 1928, *caelator* Blackman, 1928, *opimus* Blackman, 1928, and *aristatae* Bright, 1964. A review of the holotypes of all of these names plus an additional 442 specimens of these taxa, indicates that two species are represented. *Pityophthorus carinulatus* (=*opimus*) is larger (2.0–2.5 mm) and it has the pronotum and male head reticulate. The sulcus on the elytral declivity is wider, not as deep, with the tubercles on interstriae 1 and 3 finer, and the host is *Picea*. The other species, designated by the senior name *aquilus* Blackman (=*caelator*, *aristatae*), is smaller (1.8–2.1 mm), the pronotum and male head lack reticulation, the declivital sulcus is slightly deeper, with the tubercles on interstriae 1 and 3 larger, and the host is *Pinus*. Both are rather widely distributed in western North America.

Pityophthorus cascoensis Blackman, n. status

Pityophthorus cascoensis Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:99 (Holotype, female; Peak Island, Maine; U.S. Nat. Mus.)

Bright (1977, Canadian Ent. 109:515) placed in synonymy under *Pityophthorus intextus* Swaine, 1917, the names *cascoensis* Blackman, 1928, *tonsus* Blackman, 1928, *kenti* Blackman, 1928, and *pilifer* Schedl, 1931. A review of the holotypes and other type material of the above names and 1,121 additional specimens in these taxa indicates the presence of at least two and probably three species. One, represented by the type of *cascoensis* (=*pilifer*), is of larger average size (1.6–2.2 mm), the male frons is less strongly impressed and may have a weak median carina, the female frontal setae never appear scalelike, the discal interstriae are sparsely punctured, and declivital interstriae 1 bears a row of regularly spaced setae. The second species, represented by the type of *intextus* (=*shepardi, tonsus*), is smaller (1.4–2.0 mm), the male frons is rather strongly, transversely impressed and never has a median carina, the female frontal vestiture appears to include short scales when viewed with the light source coming from the direction of the beetle's vertex (an illusion caused by an abrupt curve near the base of each long frontal seta), the discal interstriae are impunctate, and the setae on declivital interstriae I are irregularly, widely spaced or absent. The type series of *kenti* is in poor condition, but is considered to be synonymous with *ornatus* Blackman, a species very closely related to *intextus.*

Pityophthorus pulicarius (Zimmermann)

Crypturgus pulicarius Zimmermann, 1868, Trans. Amer. Ent. Soc. 2:144 (Syntypes?; Lake Superior, Southern States, Tampa, and Illinois: Mus. Comp. Zool.)

Pityophthorus cubensis Schedl, 1972, Koleopt. Rundsch. 50:65 (Holotype, male; Vinales, Pinar del Río Prov., Cuba; Schedl Coll.). *New synonymy*

The male holotype of *Pityophthorus cubensis* Schedl and the 10 syntypes of *pulicarius* (Zimmermann) were compared to my series of this species. Since only one species is represented by this material the name *cubensis* must be placed in synonymy.

Pityophthorus subsimilis Schedl

Pityophthorus subsimilis Schedl, 1955, Zeit. angew. Ent. 38:25 (Lectotype, female; Ciudad Guatemala, Guatemala; Schedl Coll.)

Pityophthorus subimpressus Bright, 1977, Great Basin Nat. 36:441 (Holotype, female; 32 miles or 53 km S Valle Nacional, Oaxaca, Mexico; Canadian Nat. Coll.). *New synonymy*

The female lectotype of *Pityophthorus subsimilis* Schedl was compared directly to the type series of *subimpressus* Bright. Although the lectotype of *subsimilis* is in rather poor condition and frass obscures part of the pronotal asperities, it is clear that the asperities are essentially in obscure concentric rows. Because I see no differences in other characters, they are considered to be synonymous.

A long series of this species taken by me from a nonconiferous shrub is identical to the lectotype of subimilis. Several series of *attenuatus* Blackman from a variety of hosts in Mexico exhibit minor differences in the female frons and have the declivital punctures variable, but they are almost always smaller than in the lectotype of *subsimilis.* Because of this variability, I have regarded *subsimilis* as a minor geographical variant of *attenuatus.* However, it appears desirable to await the collection of additional material before proposing synonymy with *attenuatus.*

Premnobius cavipennis Eichhoff

Premnobius cavipennis Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2)8:404 (Syntypes; Cap bonae spei in Africa meridionalis, and Colombia; lost with Hamburg Mus.)

Premnobius latior Eggers, 1933, Trav. Lab. d'Ent. Mus. Nat. d'Hist. Nat. Mem. 1:9 (Holotype, female; St. Jean du Maroni, French Guiana; Paris Mus.)

The female holotype of *Premnobius latior* Eggers was compared directly to my series of this species from Venezuela, some of which were compared to Eggers' homotypes of *cavipennis* Eichhoff. They are obviously of the same species.

Scolytodes chapuisi, n. n.

Ctenophorus laevigatus Chapuis, 1869, Synopsis des Scolytides, p. 49 (Syntypes, two males; Colombie; Brussels Mus.)

As indicated above, the synonymy of *Scolytodes* and *Ctenophorus* has created homonyms of their type species. It is, therefore, necessary to rename the junior homonym. I propose the new name, *Scolytodes chapuisi*, as a replacement for *S. laevigatus* (Chapuis).

Scolytus propinguus Blandford

Scolytus propinguus Blandford, 1896, Biol. Centr. Amer., Coleopt. 4(6):121 (Syntypes; Mexico, Guatemala, Cuba: British Mus. Nat. Hist.)

Scolytus penicillus Schedl, 1973, Papeis Avulsos Zool. 26:165 (Holotype, male; Veracruz, Mexico: Schedl Coll.). *New synonymy*

This species is rather common in a variety of host trees from the states of Nayarit and Veracruz in Mexico to Costa Rica. Several long series in which males and females are definitely associated are in my collection. Several females were directly compared to the holotype of *Scolytus propinguus* Blandford and are identical; the males from that series are identical to the male holotype of *penicillus* Schedl. Since these names represent the opposite sexes of the same species, *penicillus* must be placed in synonymy.

Xyleborus dryographus (Ratzeburg)

Bostrichus dryographus Ratzeburg, 1837, Die Forstinsekten, p. 167 (Syntypes, female; apparently Germany; presumably Berlin Mus., not examined)

Xyleborus linearis Schedl, 1949, Rev. Brasil. Biol. 9:273 (Lectotype, female; Am. Bor.; U.S. Nat. Mus., present designation). *New synonymy*

Xyleborus linearis Schedl was named from a syntypic series in the Eggers collection, which Eggers had described but did not publish. The syntype in the U.S. National Museum is labeled "Am. Bor.; *Xyleborus linearis* n. sp. Type, Eggers det. 1927." Since it was apparently intended to be the type by Eggers and since the Schedl syntypes are on loan from the Eggers collection, I here designate the above "type" specimen in the U.S. National Museum as the lectotype of *Xyleborus linearis* Schedl. It is a specimen of the European *X. dryographus* (Ratzeburg) that was either mislabeled or intercepted in America and is not known to be established anywhere in America. The lectotype was compared directly to my series of five specimens from Europe, which were determined by Dr. A. Pfeffer.

Xyleborus horridus Eichhoff

Xyleborus horridus Eichhoff, 1869, Berliner Ent. Zeitschr. 12:282 (Syntypes, female; Teapa, Mexico; Brussels Mus.)

Xyleborus flohri Schedl, 1972, Koleopt. Rund. 50:69 (Holotype, female; Mexico; Schedl Coll.). *New synonymy*

The female holotype of *Xyleborus flohri* Schedl and the syntypes of *X. horridus* Eichhoff in the Chapuis collection were both compared directly to my series of this species. Since all represent the same species, Schedl's name must be placed in synonymy.

Xyleborus tonsus (Hagedorn), n. comb.

Dryocoetes tonsus Hagedorn, 1905, Bull. Mus. d'Hist. Nat., Paris 6:412 (Holotype, female; environs de Saint-Georges, Oyapock, Guyane française; Paris Mus.)

Dryocoetes tonsus Hagedorn must be transferred to *Xyleborus*. It represents a species group within the genus previously unknown to me.

NEW SPECIES

Araptus crassus, n. sp.

This species represents a unique group in the genus that is characterized by the very stout body form which has the general habitus of *Coccotrypes*, by the similar frons in both sexes, by the shallow, equally large strial and interstrial punctures, by the unique antennal club, and by the broad tibiae.

FEMALE(?).— Length 2.2 mm (paratypes 2.0–2.2 mm), 1.9 times as long as wide; color dark brown.

Frons evenly convex, epistomal margin with a weak, narrow, median suggestion of a premandibular process; surface smooth, shining, a very few minute, isolated granules. Antennal club obovate, about as long as scape, about 1.15 times as long as wide, and about equally divided by rather strongly procurved sutures 1 and 2, these weakly grooved and marked by rows of setae, suture 1 septate on lateral half.

Pronotum 0.94 times as long as wide; widest near base, sides strongly arcuate on basal half, rather strongly constricted, then narrowly rounded in front; anterior margin armed by about four small, indefinite granules; summit indefinite, on basal third; anterior slope rather gradual armed by low, isolated, abundant asperities extending almost to base in lateral areas, surface between asperities shining, almost smooth; posterior areas shining, not smooth, punctures very fine, indefinite, sparse. Vestiture of short, fine, recumbent hair.

Elytra 1.01 times as long as wide, 1.2

times as long as pronotum; sides straight and parallel on basal half, very broadly rounded behind; striae not impressed, punctures moderately large, distinctly impressed, spaced by diameter of a puncture; interstriae smooth, shining, almost three times as wide as striae, punctures as large as those of striae, a bit more widely spaced. Declivity broadly convex, very steep; sculpture about as on disc. Vestiture of minute strial hair, length of each less than diameter of its puncture, and erect, flattened, narrowly spatulate, closely set interstrial setae, each equal in length to about two-thirds distance between rows.

Protibia much broader than normal for this genus, armed by three major and about six minor denticles; posterior face with several granules.

Sexual differences not apparent, although both sexes apparently represented.

TYPE LOCALITY.— Eight km NE Cerro Jefe, Panama Prov., Panama.

TYPE MATERIAL.— The holotype (female?) and four paratypes were taken at the type locality on 27-III-1976, 700 m, by H. P. Stockwell.

The holotype and two paratypes are in the Canadian National Collection; the other two paratypes are in my collection.

Araptus obesus, n. sp.

This species is distinguished from the very similar *crassus* Wood by the smaller size, by the absence of a median epistomal lobe, by the more strongly impressed declivital striae, and by the yellowish brown color.

FEMALE.— Length 1.8 mm (paratypes 1.5–1.8 mm), 2.1 times as long as wide; color yellowish brown.

Frons as in *crassus* except surface more nearly subreticulate, median epistomal area with no indication of a lobe.

Pronotum as in *crassus* except asperities largely absent from posterolateral areas, punctures on posterior areas distinctly larger, setae much stouter.

Elytra as in *crassus* except declivital striae weakly impressed and interstrial punctures on 1 and 3 replaced by minute granules, interstrial setae slightly wider.

TYPE LOCALITY.— Eighteen km NE Oriximina, Brazil.

TYPE MATERIAL. The holotype (female?) and seven paratypes were taken at the type locality on 13-14-XI-1969, by J. M. and B. A. Campbell.

The holotype and four paratypes are in the Canadian National Collection; three paratypes are in my collection.

Cnesinus prominulus, n. sp.

This species is distinguished from the closely allied *minax* Schedl by the larger size, by the more slender body, by the more abundant, shorter vestiture, and by other minor details.

FEMALE.— Length 3.0 mm (paratypes: female 2.7–3.3 mm, males 2.4–3.1), 2.7 times as long as wide.

As in *minax* except as indicated above.

TYPE LOCALITY.—Volcan Colima, Jalisco, Mexico.

TYPE MATERIAL.— The holotype, allotype, and 29 paratypes were taken at the type locality on 23-VI-1965, 2500 m, No. 107, from twigs of a shrub, by me.

The holotype, allotype, and most of the paratypes are in my collection. Two paratypes are in the British Museum (Natural History).

Conophthorus conicolens, n. sp.

This species is distinguished from *apachecae* Hopkins and *ponderosae* Hopkins by the slightly stouter body form, by the more strongly, more broadly impressed declivity, with the tubercles on interstriae 3 larger, by the larger punctures on declivital striae 3, and by the smoother elytral disc, with the punctures averaging larger and somewhat confused.

FEMALE.— Length 3.7 mm (paratypes 3.3–3.8 mm), 2.2 times as long as wide; color very dark brown.

Frons and pronotum as in *mexicanus*

Wood except crenulations on pronotal disc distinctly smaller.

Elytra about as in *ponderosae* except discal punctures larger, slightly confused, declivital sulcus distinctly deeper, lateral convexities distinctly higher than suture, tubercles on interstriae 3 larger.

Male.— Similar to female except punctures on frons apparently larger.

Type Locality.— Eight miles or 13 km W Texmelucan, Puebla, Mexico.

Type Material.— The female holotype, male allotype, and 10 paratypes were taken at the type locality on 13-VI-1967, 2500 m, No. 25, from *Pinus* cones, by me. Other paratypes from Mexico include: 4 from Tlalmanalco, Mexico, 24-XI-1949, #13A, *Pinus leiophylla*, J. P. Perry, Jr.,; 2 from Tulancingo, Hidalgo, 24-VI-1953, *Pinus*, by me.

The holotype, allotype, and paratypes are in my collection.

Microcorthylus vicinus, n. sp.

This species is distinguished from *minimus* Schedl by the larger size, by the larger epistomal tubercle, by the more strongly reticulate elytra, and by the slightly narrower declivital impression.

Female.— Length 2.0 mm (paratypes 1.5–2.0 mm), 2.9 times as long as wide; color brown.

Frons as in *minimus* except epistomal tubercle distinctly larger and more nearly carinate.

Pronotum and elytra about as in *minimus* except elytra strongly reticulate, strial punctures more distinctly indicated, declivity less strongly, more narrowly impressed, lateral elevations ending more remote from costal margin.

Male.— Similar to female except antennal club without long setae on posterior face.

Type Locality.— Thirty-two miles or 51 km S Valle Nacional, Oaxaca, Mexico.

Type Material.— The female holotype, male allotype, and 34 paratypes were taken at the type locality on 21-V-1971, by D. E. Bright. Additional paratypes from Mexico include: 9 from 3 miles or 5 km N Suchixtepec, Oaxaca, on Highway 175, 4-VI-1971, 7000 ft., *Salix*, D. E. Bright; 20 from 8 miles or 13 km E San Cristobal, Chiapas, 6-VI-1969, D. E. Bright; 1 from Mt. Tzontehuiz, Chiapas, 12-VI-1969, *Quercus*, D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Pityophthorus alnicolens, n. sp.

This species is distinguished from *alni* Blackman by the smaller size, by the reticulate, dull pronotum, by the smaller, less deeply impressed strial punctures, and by the proportionately wider discal interstriae which have numerous, irregular, impressed lines.

Male (?).—Length 1.5 mm (paratypes 1.5–1.7 mm), 2.6 times as long as wide; color dark brown.

Frons broadly convex, flattened on lower half, a very feeble median carina from epistoma to upper level of eyes; epistomal margin slightly elevated; vestiture sparse, short, inconspicuous. Antennal club as in *alni* except slightly smaller, slightly more slender.

Pronotum much as in *alni* except discal area strongly reticulate, punctures coarser, margins not asperate; asperities absent from posterior third.

Elytra much as in *alni* except striae not impressed, punctures much smaller, not as deep, interstriae three times as wide as striae, with fine, irregular, impressed lines and points, with fine, rather sparse, uniseriate punctures. Declivity about as in *alni* except punctures much finer. Vestiture about as in *alni* except much longer.

Type Locality.— Highway 131, 115 miles or 184 km S Oaxaca, Oaxaca, Mexico.

Type Material.— The holotype (male?) and four damaged paratypes in poor condition were taken at the type locality on 27-30-V-1971, 6000 ft., in *Alnus*, by D. E. Bright.

The holotypes and two paratypes are in the Canadian National Collection; two paratypes are in my collection.

Pityophthorus assitus, n. sp.

This species is distinguished from *morosus* Wood by the larger size, by the stouter body, by the strongly reticulate head and pronotum, and by the more strongly impressed declivital interstriae 2.

FEMALE.— Length 2.1 mm (paratypes 1.9–2.2 mm), 2.6 times as long as wide; color dark brown.

Frons and pronotum as in *morosus* except reticulate.

Elytra as in *morosus* except strial punctures smaller, not as deep, in slightly irregular rows, a few interstrial punctures present on posterior half of disc, declivital interstriae 2 more strongly impressed on its lateral half, strial setae slightly longer.

MALE.— Similar to female in all respects.

TYPE LOCALITY.— Lagos des Colores, Chiapas, Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and 59 paratypes were taken at the type locality on 17-V-1969, by D. E. Bright. Six specimens from 15 miles or 24 km S Valle Nacional, Oaxaca, Mexico 20-V-1971, 4000 ft., D. E. Bright, are not included in the type series.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Pityophthorus concinnus, n. sp.

This species is distinguished from *coronarius* Blackman by the larger size, by the more strongly impressed male frons, and by the longer, darker, more abundant setae on the female frons.

FEMALE.— Length 1.9 mm (paratypes 1.7–2.3 mm), 2.7 times as long as wide; color dark yellowish brown.

Frons similar to *coronarius* except a bit more strongly impressed; vestiture reddish brown, longer, much more abundant; longest setae equal in length to half distance between eyes.

Pronotum and elytra as in *coronarius* except lateral convexities on declivity conspicuously higher than suture.

MALE.— Similar to female except frons rather strongly impressed from epistoma to upper level of eyes, upper margin of impressed area marked by a conspicuous, transverse carina.

TYPE LOCALITY.— “Plaquepaque, Mexico.”

TYPE MATERIAL.— The female holotype, male allotype, and 14 paratypes were intercepted at Nogales, Arizona (No. 49236) in unidentified wood from the type locality on 21-X-1941, Lot No. 41-18984. Four paratypes are labeled: Mexico, 22-III-1962, Crump Coll., unidentified wood, Boston 27132, No. 62-11725.

The holotype, allotype, and 11 paratypes are in the U.S. National Museum; two paratypes are in the Canadian National collection; and five paratypes are in my collection.

Pityophthorus indigens, n. sp.

This species is distinguished from *fuscus* Blackman by the shorter vestiture on the frons, by the more smooth, shining elytra, with smaller punctures, and by the deeper declivital sulcus.

FEMALE.— Length 2.2 mm (paratypes 2.0–2.3 mm), 2.8 times as long as wide; color very dark brown.

Frons broadly convex, a weak, median, subcarinate tubercle on epistomal margin; surface smooth, shining, punctures coarse, deep, uniformly distributed; vestiture minute, much shorter than in *fuscus*.

Pronotum about as in *fuscus* except disc smooth, shining, punctures replaced by isolated, rounded granules.

Elytra about as in *fuscus* except smooth, shining, discal punctures minute, almost obsolete, declivital sulcus distinctly deeper.

MALE.— Similar to female except median carina on frons very weakly indicated from epistoma half distance to upper level of eyes.

TYPE LOCALITY.— Two miles or 3 km E Gould, Jackson Co., Colorado.

TYPE MATERIAL.— The female holotype, male allotype, and three paratypes were taken at the type locality on 12-VI-1968, No. 8, from a *Pinus contorta* branch, by me.

Pityophthorus leechi, n. sp.

This species is distinguished from *scalptor* Blackman by conspicuous characters of the female frons as indicated below.

FEMALE.— Length 1.4 mm (paratypes 2.0–2.5 mm), 2.8 times as long as wide; color reddish brown.

Frons tranversely impressed on area below upper level of eyes, very feebly concave on median half of impressed area; surface smooth, shining, punctures moderately coarse, almost uniformly distributed, interspaces about equal to diameter of a puncture; a weak epistomal process clearly indicated; vestiture much less abundant than in *scalptor*, almost uniformly distributed, rather short, only slightly longer in marginal areas, longest setae about equal to one-third distance between eyes.

Pronotum and elytra as in *scalptor*, perhaps less brightly shining and elytral vestiture very slightly longer.

MALE.— Similar to male *scalptor* except transverse frontal impression not as strong, median carina less strongly elevated.

TYPE LOCALITY.— Two miles or 3 km NNE Angwin on N side of Howell Mt., Napa Co., California.

TYPE MATERIAL.— The female holotype, male allotype, and 27 paratypes were taken at the type locality on 5-VI-1977, reared from a shaded-out branch of *Pinus ponderosa*, by H. B. Leech.

The holotype, allotype, and some paratypes are in the California Academy of Sciences Collection; the remaining paratypes are in the Canadian National Collection and in my collection.

Pityophthorus solatus, n. sp.

This species is distinguished from *solers* Blackman by the different frons and elytra as described below.

FEMALE.— Length 2.1 mm (paratypes 1.9–2.2 mm), 2.7 times as long as wide; color very dark brown.

Frons similar to *solers* except plano-convex, punctured pubescent area extending to well above eyes, vestiture slightly more abundant and longer.

Pronotum and elytra as in *solers* except surface of elytral disc smoother, declivital sulcus slightly wider and deeper, its surface more nearly microreticulate, declivital vestiture distinctly longer.

MALE.— Similar to female except frons as in male *solers*, declivity similar to male *solers* except sulcus narrower, lateral elevation distinctly higher.

TYPE LOCALITY.— Fifty-one miles or 81 km NW Oaxaca, Oaxaca, Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and 12 paratypes were taken at the type locality on 10-V-1971, 7500 ft., *Quercus*, by D. E. Bright.

Since all allied species are from coniferous hosts, the type was probably either mislabeled or its occurrence in *Quercus* was accidental. Since Bright also collected in potential hosts at Cerro Potosí (Nuevo León) and in the Popocatépetl-Iztaccihuatl area (Mexico), it is possible that the type series was taken at a locality north of that designated; the relationship to *solers* suggests such a possibility.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Pityophthorus speciosus, n. sp.

This species is distinguished from *assitus* Wood by the smooth, shining frons which is transversely impressed on its lower half and by differences on the pronotum and elytra as described below.

FEMALE.— Length 1.8 mm (paratypes 1.7–

2.0 mm), 2.5 times as long as wide; color reddish brown.

Frons smooth, shining, punctures coarse, close, deep; transversely impressed from epistoma to slightly below upper level of eyes, upper area convex; vestiture short, inconspicuous.

Pronotum about as in *assitus* except transversely much more broadly arched, smooth, shining, with numerous, rather large, impressed points, punctures very small.

Elytra about as in *assitus* except surface smooth, brightly shining, declivital interstriae 2 strongly impressed and narrower.

MALE.— Similar to female in all respects.

TYPE LOCALITY.— Fifteen miles or 24 km S Valle Nacional, Oaxaca, Mexico.

TYPE MATERIAL.— The female holotype, male allotype, and 7 paratypes were taken at the type locality on 20-V-1971, 4000 ft., by D. E. Bright. One paratype is from 92 miles or 147 km N Oaxaca, Oaxaca, Mexico, 18-V-71, at blacklight, D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Pseudopityophthorus denticulus, n. sp.

This species is distinguished from *granulifer* Wood by the different frons, by the less definite discal striae, by the more widely spaced, more slender interstrial bristles, and by the near absence of granules and bristles on declivital interstriae 2.

FEMALE.— Length 1.9 mm (paratypes 1.6–2.0 mm), 2.9 times as long as wide; color dark brown.

Frons as in *granulifer* except more shallowly, more broadly concave, punctures smaller, more widely spaced.

Pronotum and elytra as in *granulifer* except strial punctures on disc in less definite rows, erect interstrial setae more slender, more widely spaced, spaced by distance equal to length of a seta, setae and granules absent from declivital interstriae 2, one or two granules sometimes present near base or apex on 2.

MALE.— Similar to female in all respects except antennal club sometimes more slender.

TYPE LOCALITY.— Boot Springs, Big Bend National Park, Brewster Co., Texas.

TYPE MATERIAL.— The female holotype, male allotype, and 17 paratypes were taken at the type locality on 20-VII-1974, from *Quercus*, by D. E. Bright.

The holotype, allotype, and most of the paratypes are in the Canadian National Collection; the remaining paratypes are in my collection.

Pseudothysanoes securus, n. sp.

This species is distinguished from *quercicolens* Wood by the much longer, more slender, flattened process on the female scape, by the more slender, more acutely pointed antennal club, by the more slender, more isolated pronotal asperities, and by many other characters.

FEMALE.— Length 1.5 mm (paratype 1.5 mm), 2.9 times as long as wide; color black, vestiture white.

Frons about as in *quercicolens* except surface rugose-reticulate. Scape acutely triangular, twice as wide as long, ornamented by a conspicuous tuft of rather long hair; club small, twice as long as wide, acutely pointed at apex, sutures obscure.

Pronotum about as in *quercicolens* except anterior margin unarmed, asperate area smaller, asperities smaller, more slender.

Elytra about as in *quercicolens* except strial punctures not as deep, interstriae more irregular, punctate granules larger, closer; declivital striae 1 and 2 with punctures reduced, interstriae 2 narrower, flat, 3 with weak elevation not reaching junction with 9. Vestiture white, closer, interstrial scales on disc one and one-half to two times as long as wide, on declivity about as long as wide.

TYPE LOCALITY.— Five miles or 8 km W Tulancigo, Hidalgo, Mexico.

TYPE MATERIAL.— The female holotype and one female paratype were taken at the type locality on 11-VI-1967, 2400 m, No. 12, from a *Quercus* branch, by me.

The holotype and paratype are in my collection.

Pseudothysanoes turnbowi, n. sp.

This species is distinguished from *recavus* Wood by the smoother, more brightly shining pronotum and elytra, by the less deeply, more extensively excavated female frons which has punctures and small, stout setae in the excavated area, and by the more slender scales on the male declivity.

FEMALE.— Length 1.3 mm (paratypes 1.2–1.4 mm), 2.3 times as long as wide; color very dark brown.

Frons similar to *recavus* except less strongly, more extensively impressed, surface of impressed area smooth, shining, with sparse punctures and stout setae.

Pronotum as in *recavus* except surface on posterior areas smooth, not reticulate.

Elytra as in *recavus* except smoother, interstrial setae slightly longer, more slender.

MALE.— Similar to male of *recavus* except differing by smoother frons, pronotum, and elytra and by the much more slender declivital setae, each about three times as long as wide.

TYPE LOCALITY.— Bentsen-Rio Grande State Park, Hidalgo Co., Texas.

TYPE MATERIAL.— The female holotype, male allotype, and 67 paratypes were reared from *Prosopis glandulosa* branches by Robert H. Turnbow, Jr., with emergence dates ranging from 29-31-XII-1975, 9-13, 21-23 (type), 27-29-I, 1-5, 11-18-VII, 2-8-VIII-1976. One paratype is labeled; Hidalgo Co., Texas, 26-III-57, D. J. and J. N. Knull.

The holotype, allotype, and most of the paratypes are in my collection, other paratypes are in the University of Georgia collection and the Canadian National Collection.

Pycnarthrum fulgidum, n. sp.

This species is distinguished from *lucidum* Wood by the larger size, by the less regularly punctured pronotum, by the smaller, less strongly impressed punctures on the elytral striae, and by the much finer vestiture.

MALE.— Length 1.8 mm, 2.0 times as long as wide; color brown.

Frons shallowly, broadly, transversely impressed, not concave; surface shining, slightly irregular, punctures fine, rather sparse, not clearly defined; vestiture short, rather sparse, almost hairlike. Eyes more finely faceted and more widely separated than in *lucidum*.

Pronotum much as in *lucidum* except slightly more declivous on anterior third, surface not as smooth, punctures slightly larger, not as regular in size. Elytra somewhat as in *lucidum* except striae not impressed, punctures much smaller, less strongly impressed, interstriae three to four times as wide as striae, ground vestiture very sparse, hairlike, as fine as strial setae, except interstrial setae slightly longer and much more slender than in *lucidum*, not stouter on declivity.

FEMALE.— Similar to male except frons convex.

TYPE LOCALITY.— Eight km S Colonia, Valle de Cauca, Colombia.

TYPE MATERIAL.— The male holotype, female allotype, and seven paratypes were taken at the type locality on 9-VII-1970, 30 m, No. 650, from *Guarea trichiloides*, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes fulmineus, n. sp.

This species is distinguished from *amabilis* Wood by the larger size, by the more strongly reticulate pronotum, with finer punctures, and by the very different female frons.

FEMALE.— Length 1.8 mm (paratypes 1.6–1.8 mm), 2.4 times as long as wide; color black.

Frons weakly convex from epistoma to above upper level of eyes, median third smooth, shining, impunctate, lateral thirds rather finely, closely punctured; vestiture confined to punctured areas, fine, short, longest setae about equal in length to diameter of three facets of eye.

Pronotum about as in *amabilis* except surface strongly reticulate, punctures much smaller but slightly larger than in *clusiae* Wood.

Elytra as in *ambilis* except vestiture confined to odd-numbered interstriae, not more than three or four setae on each of these.

MALE.— Similar to female except frons more strongly convex, punctures rather sparse, uniformly distributed, vestiture sparse, inconspicuous.

TYPE LOCALITY.— La Carbonera Experimental Forest, about 50 km (airline) NW Merida, Merida, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 11 paratypes were taken at the type locality on 14-X-69, 2500 m, No. 50, from *Clusia* branches, by me.

Scolytodes radiatus, n. sp.

This species is distinguished from *clusiae* Wood and *volcanus* Wood by the slightly larger size, by the much coarser pronotal punctures, and by the very different female frons.

FEMALE.— Length 1.7 mm (paratypes 1.6–1.9 mm), 2.4 times as long as wide; color almost black.

Frons convex and virtually glabrous as in males of allied species.

Pronotum much as in *volcanus* except punctures much larger, each equal to from half to full diameter of a strial puncture (variable).

Elytra about as in *amabilis* Wood except punctures larger and vestiture less abundant; striae not impressed, punctures rather coarse, deep; interstriae slightly wider than striae, smooth, shining, punctures uniseriate, less than half diameter of those of striae. Subglabrous, a few fine setae on odd-numbered interstriae on posterior half.

MALE.— Similar to female in all respects.

TYPE LOCALITY.— La Georgiana, 79 km SE San José, Costa Rica.

TYPE MATERIAL.— The female holotype, male allotype, and 13 paratypes were taken at the type locality on 31-VII-1965, from *Quercus*, by L. S. Otvos.

The holotype, allotype, and paratypes are in my collection.

Xyleborinus tribuloides, n. sp.

This species is distinguished from *bicornatulus* Wood by the uniformly reticulate pronotum and by the much shorter, less strongly impressed, very different declivity.

FEMALE.— Length 2.1 mm (paratype 2.3 mm), 2.9 times as long as wide; color dark brown.

Frons and pronotum about as in *bicornatulus* except pronotal disc uniformly, strongly reticulate.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; declivity confined to posterior third; striae not impressed, punctures fine, shallow; interstriae smooth, shining, three to four times as wide as striae, punctures finely granulate. Declivity gradual, shallowly subconcave; punctures on striae 1 and 2 slightly larger than on disc; interstriae 1 and 2 unarmed except for small granules at base, 3 armed one-third declivital length from base by a moderately coarse, pointed tubercle, as high as wide, a larger, blunt spine two-thirds of declivital length from base, longer than wide, its length about equal to width of an interstriae, a small tubercle at base above spine 1 and another at apex below spine 2; lateral summit at striae 4, lateral areas armed by about a dozen moderately coarse tubercles (smaller and less numerous than in *bicornatulus*. Vestiture of minute strial hair and distinctly longer interstrial hair, regularly, closely spaced to base, each interstrial seta about equal in length to width of an interstriae.

TYPE LOCALITY.— Fifteen miles or 24 km S Valle Nacional, Oaxaca, Mexico.

TYPE MATERIAL.— The female holotype and one female paratype were taken at the type locality on 20-V-1971, from a *Cecropia* petiole, by D. E. Bright.

The holotype is in the Canadian National Collection; the paratype is in my collection.

Xyleborus devexus, n. sp.

This species is distinguished from *obliquus* (LeConte) by the smaller size, by the coarser, deeper elytral punctures, and by the absence of tubercles on declivital interstriae 1 and 3.

Female.— Length 1.9 mm (paratypes 1.8–2.1 mm), 2.5 times as long as wide; color very dark brown.

Frons and pronotum as in *obliquus*.

Elytra as in *obliquus* except declivity slightly steeper, less strongly convex; punctures on disc larger, deeper, interstriae twice as wide as striae; interstrial punctures near declivity not granulate. Declivity more distinctly impressed between interstriae 3; interstriae 1-3 without granules. Vestiture as in *obliquus*.

Type Locality.— Homestead, Florida.

Type Material.— The female holotype and three female paratypes were taken at the type locality on 27-X-1957 on Burdiken palm. Additional female paratypes were taken as follows: 3 from Orange Heights, Florida, 3-V-1914, Hopk. US 9925i, pecan, E. W. Berger; 1 from Lake Co., Florida, 21-I-1930, B. L. Smith; 1 from Manatee Co., 2-IV-1930, R. F. Tinker; 1 from Orange Co., Florida, 24-I-1930, W. M. Loe; 1 from Orange Co., Florida, 22-III-1930, J. E. Sadler; 2 from Pinellas Co., Florida, 22-III-1930 and 12-IV, B. P. Moore; 15 from Río Grande, Puerto Rico, 26-IV-1940, *Cedrella mexicana*, Hopk. US 33100-V-1, D. DeLeon; 4 from Vega Alta, G. N. W. (presumably Puerto Rico), 16-XI-1915, acc. no. 170-15.

The holotype and several paratypes are in my collection; the remaining paratypes are in the U.S. National Museum of Natural History.

Xyleborus laticeps, n. sp.

This species is distinguished from *retusus* Eichhoff by the slightly smaller size, by the nonreticulate, much more coarsely punctured pronotal disc, and by the different declivity as described below.

Female.— Length 3.5 mm (paratypes, females 3.1–3.6 mm, males 1.7–2.0 mm), 1.7 times as long as wide; color black.

Frons as in *retusus* except more coarsely punctured.

Pronotum as in *retusus* except posterior areas usually smooth, shining, coarsely, closely punctured, interspaces in discal area equal to about half diameter of a puncture (reticulate and equal to two to four diameters in *retusus*).

Elytra as in *retusus* except discal punctures slightly larger, margin of declivity with a subacutely elevated circumdeclivital ring forming a complete circle (forming about two-thirds of a circle in *retusus*), punctures on declivital face at least twice as large, surface with few to many irregular, serpentous impressed lines (these lines absent in *retusus*).

Male.— Similar to female except dwarfed, deformed; pronotum and elytra more gradually declivous; all features less sharply defined.

Type Locality.— Twenty km SW El Vigía, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 33 paratypes were taken at the type locality on 21-XI-69, 50 m, No. 145, from *Jacaranda* poles, by me. (The allotype and 17 of these paratypes were reared at and incorrectly labeled Merida, 22-IX-69, 1700 m.) Additional paratypes from Venezuela include: 12 from 9 km S Barancas, Barinas, 1-X-69, 150 m, No. 24, *Protium tenuifolium*, 9 more with the same data except 5-XI-69, *Inga* sp., *Spondias mombin*, or *Dendropanax arboreum*, 1 more with the same data except 2-XII-69, *Melicoccous bijugata;* 1 from 17 km SE Mirí, Barinas, 17-XII-69, 150 m, No. 195, *Protium;* 1 from 10 km SE Mirí, 8-II-70, 150 m, No. 295, *Inga;* 3 from 8 km SW Bumbum, Barinas, 11-II-70, Moraceae, *Protium tenuifolia*, or "Tartaguito"; 6 are from 40 km E Canton, Barinas, 8-III-70, from various hosts or in flight; all were taken by me. Three paratypes are from Valle de Choroni, Venezuela, 3-IV-1964, *Theobroma cacao*, J. L. Saunders.

The holotype, allotype, and paratypes are in my collection.

SUPPLEMENTARY NOTE ON VENEZUELAN BAT FLIES (DIPTERA: NYCTERIBIIDAE)

Lindolpho R. Guimarães[1]

Abstract.— *Basilia dunni* Curran (1935) is reported from Venezuela for the first time, and comments are made on four other indigenous species.

After the publication of *Venezuelan Nycteribiid Bat Flies* (Guimarães 1972) I received 17 additional vials with 33 specimens of nycteribiids from Dr. Vernon J. Tipton. They were collected in the same area where the previous collection was made. The cumulative total number of specimens collected by the personnel of the Smithsonian Venezuelan Project (SVP) is 166, from 94 host specimens. There are five species represented in the new material, of which one had been recorded previously from Venezuela and one, *Basilia dunni* Curran (1935), is reported for the first time.

Basilia anomala Guimarães and D'Andretta, 1956

Fig. 1

Basilia anomala: Guimarães, 1972: 1

Present record.— One female ex *Rhogeessa tumida* (SVP 11109), Miranda: 5 km E Rio Chico, near Puerto Tuy, 6-XI-1966.

Remarks.— This is the second known female of the only South American species with three tergal plates.

The abdomen of the female figured in the original description (Guimarães and D'Andretta 1956) was swollen, and so somewhat different from the specimen figured herein, chiefly with regard to the shape of tergal plates I and III. In this specimen, the abdomen is rather shrunken, the lateral margins of tergal plate I are rolled up, and the posterior margin looks bilobate, due to a notch on the midline; viewed under the stereomicroscope, the midline of the tergite appears depressed. Tergal plate III is more regular: the lateral margins converge toward the back, and the posterior margin is slightly emarginate.

Basilia dubia Guimarães and D'Andretta, 1956

Basilia dubia: Guimarães, 1972: 3

Present records.— Two females, ex *Myotis albescens* (SVP 16173), Amazonas:

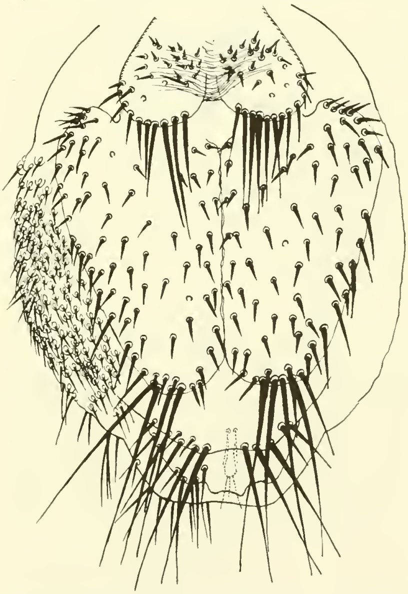

Fig. 1. *Basilia anomala*, abdomen of female, dorsal view (SVP 11109).

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Belém, Rio Cunucunuma, 150 m elev., 1-II-1967; 3 females and 2 males, ex *Myotis albescens* (SVP 16210), Amazonas: Belém, Rio Cunucunuma (mouth Caño Culebra), 150 m elev., 2-II-1967; 3 females, ex *Myotis albescens* (SVP 19515 and 19634), Amazonas: 1 km down Casiquare Canal from Capibara, 130 m elev., 6-VI-1967 and 13-VI-1967.

REMARKS.— The characters that distinguish this species from *B. carteri* show some variability. The females mentioned in my 1972 paper had a less cordiform tergal plate I than specimens previously known; one specimen, from Apure, had no pustulate setae on the lateral connexivum. Among the females now examined, the majority of which have tergal plate I perfectly cordiform, I found one specimen with the margin truncate, and one specimen with a much more elongate plate than the others. In some specimens the pustulate setae of the lateral connexivum are so few (3-4) and so small that they are hardly visible.

Basilia ferrisi Schuurmans-Stekhoven, 1931

Basila ferrisi: Guimarães, 1972: 7

PRESENT RECORDS.—One female (SVP 43462) ex *Myotis simus*, Monagas: Mata de Bejuco, 54 km SE Maturin, 18 m elev., 3-VI-1968; two females (SVP 44232), ex *Myotis nigricans*, Falcon: Capatárida, 40 m elev., 26-VI-1968.

Basilia dunni Curran, 1935
Fig. 2

Basilia dunni Curran, 1935: 3, Figs. 1, 2; Scott, 1936: 497 (citation); Del Ponte, 1944: 118, 124 (citation and key); Guimarães, 1946: 16, 20 (citation and key); Guimarães and D'Andretta, 1956: 26 and 95, Figs. 152, 153 (key and redescription of holotype); Maa, 1965: 380 (included in the subgenus *Pseudelytromyia*); Guimarães, 1966: 399, Fig. 37 (comments and description of male) Guimarães, 1968: 101.2 (citation).

PREVIOUS RECORDS AND HOSTS.— Panamá: Santa Rosa, ex *Myotis nigricans* (holotype); Canal Zone, Juan Mina, ex *Myotis n. nigricans;* Darien, Rio Tuira, ex *Myotis albescens.*

PRESENT RECORDS.— Five females (SVP 29146 and 29149), ex *Myotis albescens*, Amazonas: almost directly across Rio Manapiare from camp, 155 m elev., 26-VII-1967; two females (SVP 30603), ex *Myotis albescens*, Amazonas: Paria, 25 km SEE Puerto Ayacucho, 114 m elev., 13-IX-1967.

REMARKS.— *B. dunni* is here recorded for the first time from Venezuela; it was known only from Panamá. The holotype was found on *Myotis nigricans*; all other records were from *Myotis n. nigricans* (1) and from *Myotis albescens* (4).

The two figures of the female of this species (Curran 1935, Guimarães and D'Andretta 1956) were based on the holotype. In the specimen now figured the discal setae of tergal plates I and II are fewer than in the holotype. The male was described and figured by me in 1966.

In my key to females of Venezuelan species of *Basilia* (Guimarães 1972) *B. dunni*

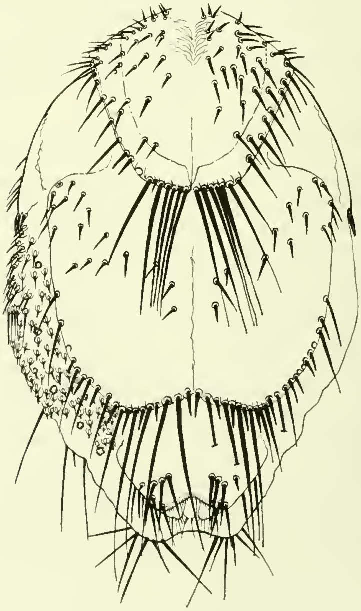

Fig. 2. *Basilia dunni*, abdomen of female, dorsal view (SVP 29146).

should appear in the last couplet, after *B. ferrisi*, as follows: "Tergal plate II with discal setae in irregular rows converging obliquely toward the midline; longer setae of posterior margin of tergal plate I not reaching the posterior margin of tergal plate II."

Basilia ortizi Machado-Allison, 1963

Figs. 3, 4, 5

Basilia ortizi: Guimarães, 1972: 2

PRESENT RECORDS.— Five males and seven females ex *Eptesicus* (SVP 25562A, 26765, 26767, 26768, 26770, 26771, and 26773), Amazonas: San Juan, Rio Manapiare, 155 m elev., 9 and 15-VII-1967.

REMARKS.— As previously noted (Guimarães 1972), this species closely resembles *B. bequaerti*. It is indeed difficult to believe that it is a good species, but only the examination of specimens from the same host and area will allow a firm decision.

On the basis of the specimens seen, it seems to me that the setae of the lateral connexivum, especially the outer ones, are a little longer in *B. ortizi* than in *B. bequaerti*. The posterior processes of tergal plate II are narrower in *ortizi*, although not as thin as those of *B. wenzeli*.

The number of setae on this process is also quite variable. Guimarães and D'Andretta (1956) state that *B. bequaerti* has from four to six spiniform setae and from two to four long and robust setae.

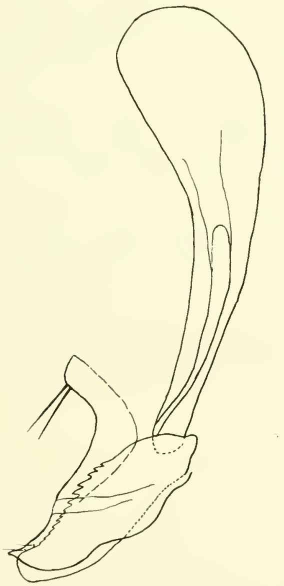

Fig. 3. *Basilia ortizi*, spiniform setae of the posterior margin of the fourth visible sternite of the male.

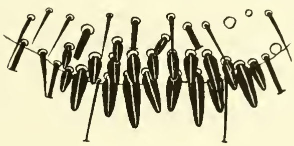

Fig. 4. *Basilia ortizi*, genitalia of the male, lateral.

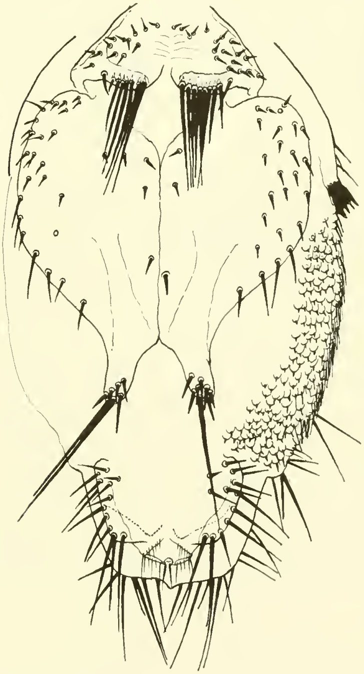

Fig. 5. *Basilia ortizi*, abdomen of the female, dorsal view (SVP 26771).

They illustrate one specimen with six spiniform setae and three long setae on one of the processes and, respectively, four and four on the other. The drawing of the type by Machado-Allison (1963) shows three spiniforms on one side and four on the other, and two long setae on either side. The specimens I am identifying as *ortizi* have at most two long setae; the specimen now figured has two spiniform and two long setae on one side, respectively, and seven and one on the other side.

Differences in the posterior elevation of the mesonotum and in the shape of the anal segment are probably due to preservation.

In the figured female the genital and adanal plates are similar to those of *B. bequaerti*.

The aedeagus of the figured male resembles that of *B. bequaerti* in the serration of the dorsal margin, but its distal end is thicker, while the parameres are much thinner distally than in *B. bequaerti*. However, since little is known of the variability of the male genitalia in *Basilia*, the significance of the differences mentioned is not clear.

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THE SYSTEMATICS OF *CROTAPHYTUS WISLIZENI*, THE LEOPARD LIZARDS. PART III. THE LEOPARD LIZARDS OF THE GREAT BASIN AND ADJOINING AREAS, WITH A DESCRIPTION OF A NEW SUBSPECIES FROM THE LAHONTAN BASIN

Wilmer W. Tanner[1] and Benjamin H. Banta[2]

Abstract.—A general analysis of the populations of *Crotaphytus wislizeni* in the Great Basin is presented. A new subspecies, *C. wislizeni maculosus*, for the Lahontan Basin, Nevada, is described and comparisons of color pattern, some scale patterns, and skull measurements are presented.

In Part I of this series we (Tanner and Banta 1963) reported the taxonomic status of *Crotaphytus wislizeni wislizeni* and described the subspecies *C. w. punctatus* from the Upper Colorado River Basin. Part II (Banta and Tanner 1968) dealt with the leopard lizards of Baja California, Mexico, with the description of the subspecies *C. w. neseotes* from Cedros Island. The present study is concerned with the taxonomy of the populations occurring in the Great Basin and adjoining areas west of the Colorado River. With a few exceptions, leopard lizards from this large area have been referred to as *C. w. wislizeni*. However, we note real differences between some populations in this area and those seen from areas to the east (Arizona and eastern Utah), the south (Baja California), and the west (Central California).

The Great Basin is a large geographical area lying between the Rocky Mountains and high plateaus of central Utah on the east and the Sierra Nevada Mountains to the west. Ingress into this area has occurred from the south and southeast with lizards from the southern deserts extending their ranges northward either along the desert ranges or the alluvial valleys. The leopard lizards have used the desert valleys to extend their ranges as far north as southern Oregon and southwestern Idaho.

Specimens from the Great Basin seen by us while preparing the two previous reports were reexamined, and the data are now being added to that pertinent to this report. We have received on loan from Dr. John Wright, Los Angeles County Museum (LACM), a large series of specimens from the southern parts of the Great Basin. These and those seen from other collections (see previous reports) form the basis for this study. Several collections have been made by the authors or their students, in areas not well represented by existing collections, for the purpose of procuring live material. We are grateful to the following for materials sent on loan from critical areas: Mr. James Davis, Indio, California; Dr. Steven C. Anderson, Pyramid Lake, Nevada; Dr. Nathan M. Smith, southern Idaho and southern California; and Mr. M. L. Abts, south central Oregon. Specimens from the Nevada Test Site were obtained by the senior author as a part of the Atomic Energy Commission Grant AT (11-1)-819. Other colleagues and students have aided in the field work and have provided data and suggestions for which we are most appreciative. We are grateful to Drs. Robert C. Stebbins and David Wake for the privilege of examining the extensive collections at the University of California at Berkeley (MVZ), and to Dr. Alan E. Leviton for the opportunity to examine or receive on loan specimens from the California Academy of Sciences (CAS). We are also grateful for the privilege of studying specimens from the Field Museum of Natural History (FMNH), University of Michigan (UM), University of Kansas (KU), and the U.S. National Museum (USNM).

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Perhaps the first report dealing with the leopard lizards of the Great Basin was the notes of C. Hart Merriam (Stejneger 1893), which include observations of these lizards from southwestern Utah, southern Nevada, and east, central, and southern California. Since the report by Stejneger (1893), many articles have referred to the leopard lizards of the Great Basin. However, in none of these is there any change in the taxonomy, since all references refer to *Crotaphytus wislizeni*.

Aside from our previous reports (parts I and II) most other studies have included the leopard lizard as a part of a distribution list or as a part of ecological or natural history notes (Taylor 1912, Richardson 1915, Van Denburgh 1922, Knowlton et al. 1934, 1936, 1946, Allred, Beck, and Jorgensen 1963, Banta 1963, Jorgensen and Tanner 1963, Stebbins 1966, Fitch 1970). Montanucci (1970) analyzed the relationship between the leopard lizards of the central valley of California (*C. w. silus*) and those adjoining populations (*C. w. wislizeni*) in northern Los Angeles and eastern Kern counties, California. In this report on this species we will discuss and characterize those populations occurring in the Great Basin and attempt to indicate the zones of intergradation, as well as the presumed lanes of migration into the present area of distribution.

Those populations in southern California (Imperial, Riverside, and San Bernardino counties) include individuals with varying expressions of the color pattern seen in *C. w. wislizeni* in Arizona and New Mexico. There is a strong tendency for the spots to be smaller and for the rings of white spots to be reduced or absent so that in some large females the pattern is greatly faded and the spots reduced in size and number. In adjacent northeastern Baja California the few specimens seen are similar and do not indicate any influence from *C. w. copei.* However, those examined from western Sonora (Kino Bay) have dorsal patterns as typical for *C. w. wislizeni* as those from south central Arizona.

In southern and eastern Nevada the trend is toward smaller spots. This also occurs in southwestern Utah, where many individuals are patterned similar to *C. w. punctatus* of eastern Utah. There is a reduction in the numbers of postmentals from southeastern Utah to southwestern Utah and adjoining eastern Nevada. This same pattern exists in much of east central Nevada and the Great Basin of western Utah.

An explanation of the lanes of dispersion used in reaching this large area and the taxonomic explanation of the population diversities are not clear. If we assume that the species had its origin in the desert plateaus of central or north central Mexico, then the following may be an initial attempt at an explanation of what we now see: at the close of the last thrust of the Pleistocene ice age the distribution of *Crotaphytus wislizeni* must have been restricted primarily to the drier, warmer areas of northern Mexico and perhaps some adjoining areas of the southwestern United States. We have no evidence that the leopard lizard populations now extant were isolated as a result of the several ice flow advances or extensive pluvial lake formations. Because of their general morphological similarity and the zones of intergradation occurring between populations, we consider the present distribution of this species to have been etablished since the Pleistocene.

As the areas to the north and west warmed and dried, these lizards dispersed into the desert valleys formed between the mountain ranges south of the high plateaus in central Arizona and western New Mexico. The first range extensions into this area must have been into the lower valleys extending westward to the Colorado River and northward into the Rio Grande Valley. As the warming trend continued, higher elevations and the more northern areas became occupied. Perhaps at this time the range was rapidly extended up the Rio Grande Valley in New

Mexico, and thus onto the plateaus of New Mexico, Arizona, western Colorado, and Utah. By entering such areas through low areas in the terrain, some populations were removed by distance and partially isolated fom the main body of the species. This reduced gene flow and the new and different habitat resulted in adaptive changes in some of the fringe populations, which we now recognize as sufficiently distinct to warrant subspecies designation.

Two basic color patterns exist east of the Colorado River and in northwestern Mexico. Those populations in the low valleys north and south of the U.S.-Mexican border are *C. w. wislizeni*, and those in the high plateaus (mostly upper Colorado River drainage north and east of Grand Canyon) are *C. w. punctatus*. The northeastern population of *C. w. punctatus* has reduced pigmentation on the dorsum; small, widely dispersed spots; narrow, light cross bands; and an increase in the number of postmentals. If one travels south from the San Juan River of Utah into Arizona and New Mexico the characteristics are modified by an enlargement of the spots and a decrease in the number of postmentals. The zone of intergradation between *C. w. wislizeni* and *C. w. punctatus* is wide, and no attempt is made to define its precise limits. The dorsal spots do increase in size from southeastern Utah across the plateaus south and east into Arizona and New Mexico. In spite of the steep canyons and swift rivers in the Upper Colorado Basin, these leopard lizards have succeeded in crossing them and are established on the west side of the Colorado and Green Rivers in Utah and northern Arizona. From this position they have moved westward from the Colorado River through the gap between the Kaibab Plateau to the south and

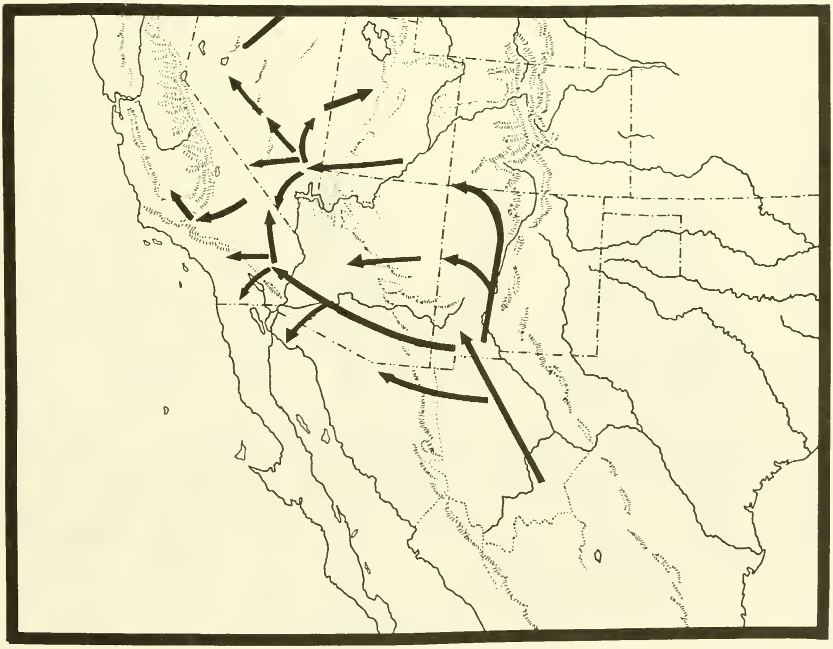

Fig. 1. Possible routes of leopard lizard movement from the ancestral stock to their present distribution since the Pleistocene.

the Paunsaugunt Plateau to the north, to reach the Virgin River drainage in southwestern Utah and southeastern Nevada.

If the above hypotheses are correct, the Great Basin was invaded by leopard lizards originally derived from two populations: 1) Those moving westward through the desert valleys of southern Arizona which crossed the Colorado River, entered southern California, and extended their range south into Baja California Norte and west and north into the Great Basin. 2) Those moving west in southern Utah entered Nevada, where they also expanded south, west, and north into the Great Basin (Fig. 1).

An examination of the populations now extant in southwestern Utah, southeastern Nevada, and southern California show a wide zone of intergradation between these two basic population types (*C. w. wislizeni* and *C. w. punctatus*). A large series from the Nevada Test Site (Mercury, Frenchman, Jackass, and Yucca valleys) contains examples of both of the subspecies indicated above and many color patterns intermediate between them (Fig. 2). The populations in southern Nevada apparently represent a major area of intergradation. As one samples populations to the north and east into extreme eastern Nevada and the Great Basin of Utah, the characteristics of *C. w. punctatus* are strongly evident but with an occasional representative of *C. w. wislizeni* pattern and individuals with intermediate characteristics. To the south particularly, and southwest of the Nevada Test Site, individuals with *C. w. wislizeni* characteristics are seen more often. We are also impressed with the general differentiations in these populations brought about perhaps not only by introgression (hybridization) but also by the natural selection processes. Although most of the valleys in the Great Basin are interconnected either through low passes in the mountain chains or are connected at one or both ends of the discontinuous ranges, there are factors which bring about varying degrees of isolation. In some valleys the effects of isolation and thus some differentiating characteristics are more apparent. This is most obvious in the fringe areas such as the Lahontan and Humboldt valleys in northwestern Nevada, the adjoining areas in northeastern California, southern Oregon,

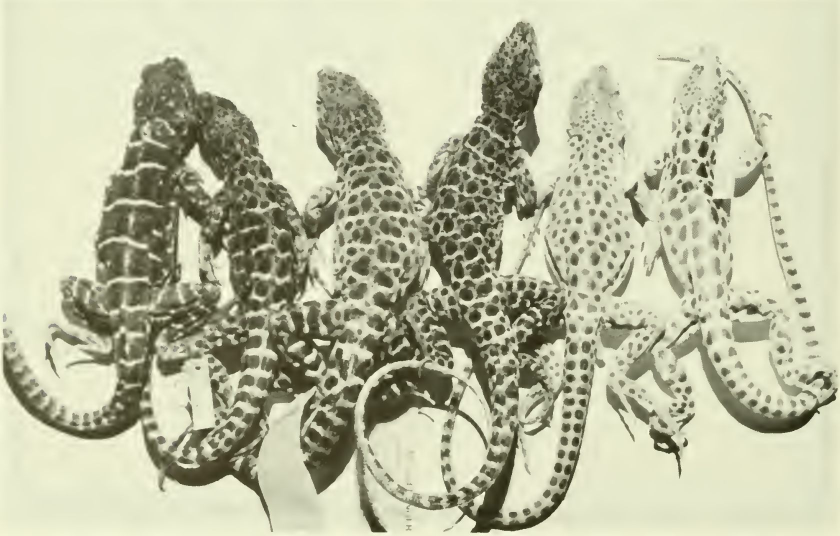

Fig. 2. Individuals showing color pattern variations.

and the Snake River Valley of southwestern Idaho. The population in Antelope Valley (Los Angeles County) also shows some distinct color pattern characteristics which seem to represent some degree of intergradation with the *C. w. silus* population in the San Joaquin Valley.

Montanucci (1970) contends that there is sufficient differentiation between *silus* and the adjoining populations to the south and east to justify full species rank for *silus*. He found that the skull in the *silus* population was shorter than for other *C. wislizeni* populations, and the color pattern is distinct. Furthermore, few intergrades were found nor were there recognizable areas of overlapping for the populations in question.

We have examined a large series of specimens from the south end of the San Joaquin Valley as well as available specimens from along the Tehachapi Mountains from Mojave, both north and south. West from Lancaster and Palmdale, Antelope Valley slowly rises in elevation and narrows as it approaches Frazier Park (at about 3,500 feet) just north of Tejon Pass. On the basis of specimens seen from Antelope Valley, Frazier Park, Grapevine Canyon, and to the west and north of Wheeler Ridge, there is apparently a narrow route into the south end of the San Joaquin Valley. Furthermore, at Frazier Park we find intergrades (CAS 12787-8 and 1243). In northeast Kern County a specimen (CAS 93427) from 1.3 mi W of Cane Wells (7 mi SE of Weldon) has a color pattern very similar to individuals from Washoe County, Nevada. There are other low passes along the Tehachapi Mountains through which entrance into the San Joaquin Valley may have occurred.

We agree with Montanucci (1970) that intergrades are not common between *C. w. silus* in the Central Valley and those populations of *wislizeni* to the south and east. This does not suggest, however, that the two populations will not produce fertile offspring in nature or (and) that the adaptive changes in the color pattern and length of the skull are entirely the result of a gene flow so reduced as to produce reproductive isolation. There is no question that the population in the San Joaquin Valley, once established, received only a limited gene flow from the adjacent populations. The nature of the terrain was apparently the principal factor responsible for this reduction, although in recent years human activities south and east of Bakersfield, Kern County, have so altered the habitat that this lizard no longer occurs in wide areas. By eliminating leopard lizards fom the areas between the Tehachapi Mountains and Bakersfield, that portion of the population in the San Joaquin Valley most likely to show intergrading characters was also eliminated. There appears to be only one possible area in which there might still be contact between the two populations. That area is from the west end of Antelope Valley, then along the foothills westward to the Pleito Hills and Wheeler Ridge. Even this contact may have been seriously disrupted or closed by recent highway construction.

The entire area extending westward from southern Nevada serves as a potential route of dispersion toward the low passes from the Mojave Desert and into the southeastern end of the San Joaquin Valley of California. This route leads directly into Antelope Valley and the areas south and east of Bakersfield. Extensive agriculture in the south end of the valley has effectively established an artificial barrier between these populations. All of this is, however, very recent, certainly within the last century. There is no reason to suspect that noticeable genetic changes in these populations have occurred in the time since man intervened.

It should be noted that Montanucci (1970) reported some overlap of the skull character between *silus* and other populations of *wislizeni*. Smith and Tanner (1974) found that the collared lizards in the Great Basin (*C. collaris bicinctares*) also was distinguishable from other *C. collaris* subspecies on the basis of cranial anatomy (ratio of width to length). Similarly, we must recognize the possibility that there is proportional variation in the length and width of the skull in the genus *Crotaphytus*. Furthermore, we question the validity of species/subspecies based on the estimated amount of gene flow between populations. If this is important (and we agree that it plays a role in such deliberations), then what should be done with the numerous insular subspecies in Baja California where gene flow is nil or absent?

We have weighed the pros and cons of species vs. subspecies in this case and can recognize strengths in both alternatives. The occurrence of recognizable intergrades reported by Montanucci (1970) and among the specimens we have seen (even though the intergrades in each study are few in number) is a strong deterrent to the recognition of *silus* as a species. Furthermore, what is to be gained by splitting? We are persuaded, as was Simpson (1945), that such splitting may tend to destroy or dim the true relationship between these populations rather than to establish the basic position of each to each other. We, therefore, retain the leopard lizards in the San Joaquin Valley of California as a subspecies of *Crotaphytus wislizeni* until sufficient data become available to justify the elevation of *silus* to full species status.

The populations in the Great Basin exhibit considerable variation if one examines material from the Salton Sea Basin north into the Lahontan Basin of northwestern Nevada. There are, in fact, two populations with rather distinct color patterns. Those seen from the Coachella Valley south have a faded pattern. This is particularly true for adult females, in which some have few or no spots or bars. In males the pattern is more evident and often reflects traces of the pattern seen in Arizona specimens. Obviously a distinct pattern has not been established, and what we are seeing should be considered, for the present at least, as a developing pattern resulting from adaptive change in the new habitat resulting from partial isolation, but with some influence from the populations to the north and east.

The color pattern throughout a wide area in parts of northern and eastern Riverside County, most of San Bernardino County, eastern Inyo County, California; and in southern Nevada is extremely variable. Nearly all of the color patterns seen in this species have been observed in specimens from the Nevada Test Site, except for the typical *silus* pattern. This wide area of variability is apparently maintained by continuous gene flow from the northeast (*C. w. punctatus*) and from the southeast (*C. w. wislizeni*). The phenotypes in Fig. 2 are indicative of a large and varied gene pool, which under selective environmental conditions has the potential to produce a wide variety of color patterns.

In contrast to the south and central parts of the Great Basin, the north and western areas comprising the Lahontan Basin and the Snake River Basin from Ada County south and east to at least Bannock County, Idaho, have evolved a distinct color pattern. The most striking variation is in the size and shape of the spots. Because of the large distinct spots, we propose it be known as:

Crotaphytus wislizeni maculosus, subsp.

Figs. 3, 4d

HOLOTYPE.—An adult male, BYU 32685, taken approximately 200 m W of the lookout point along Nevada Highway 33, west side of Pyramid Lake, Washoe County, Ne-

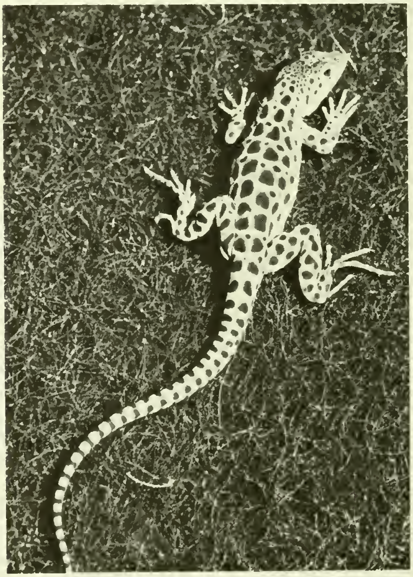

Fig. 3. Dorsal view of the holotype of *Crotaphytus w. maculosus*. BYU 32685, taken on the west side of Pyramid Lake, 24 July 1970.

vada, by Wilmer W. Tanner, on 24 July 1970.

PARATYPES.—Nevada: Washoe County: Topotypes (BYU 32686-7); Pyramid Lake, near south end (BYU 36405-8); Pyramid Lake (CAS 40507-9, 40516-26, 40533-5, and 44157). Idaho: Owyhee Co.: 17 mi SW Nampa, Hwy 78 (BYU 40676-7, 40773, 40815), 14 mi S. Bruneau (BYU 32706); Gooding County: 5.5 mi S. Gooding (BYU 32699-701), 5 mi N. Wendell (BYU 32697-8 and 32704-5); Ada Co.: Foothills N. Boise (SDHNM 1450-2, 23636 and CAS 45426-27, 53775-80).

DIAGNOSIS.—A subspecies of *Crotaphytus wislizeni* most closely related to *C. w. punctatus* and *C. w. wislizeni* to the south and east of its distribution. Distinguished from *C. w. punctatus* and *C. w. wislizeni* in that the dorsal spots are greatly enlarged in size and often quandrangular rather than round. *C. w. maculosus* is distinct from *C. w. punctatus* in having fewer postmentals and greatly enlarged spots and from *C. w. wislizeni* in that there is not a circle of white dots around the larger dorsal spots. In contrast to *C. w. silus* the enlarged dorsal spots are distinct on each side of the middorsal line and between the transverse bars. Individuals have not been seen with the entire dorsal area between the bars pigmented as in most *C. w. silus*.

DESCRIPTION OF TYPE.—An adult male, snout to vent 94 mm, total length 283 mm, tail total length ratio 1.49; dorsal scales (occipital to base of tail) 187; ventrals 93, noticeably larger than laterals and dorsals; scales around middle of body 162, middorsal rows not noticeably enlarged, beadlike; supralabials 16-17; infralabials 16-18; femoral pores 19-20, 2 or 3 small scales on posterior margin of pore; 20 scales between femoral pore series; head scales from rostral to occiput 22, smooth, occiput largest dorsal head scale, but with row of 8 enlarged scales from rostral posteriorly; postmentals 2-2; scales on anterior two-thirds of tail smooth, posterior scales weakly keeled. Head scales smooth, platelike, some raised medially, none imbricate; gulars enlarged near labials, smaller medially, and slightly longer than wide; gular fold prominent; scales posterior to fold enlarged and these in about 40 longitudinal rows.

Head distinct, 22 mm long, 16.5 mm wide; rostral to ear 22 mm; body slightly flattened, wider than high; longest toe 20 mm. Color pattern consisting of a series of six rows of large dark brown spots extending from head and shoulders to base of tail, middorsal rows and one lateral row extending onto tail; a series of 9 spots in middorsal rows from nape to base of tail, spots from 10 to 12 mm long, from 8 to 10 wide, and involving from 12 to 16 rows of dorsal scales; lateral spots smaller; transverse bars not distinct, confused with light areas surrounding the enlarged spots; gular region marked with several parallel dark, longitudinal stripes extending from labials to posterior edge of ear, a few spots between median strip and first lateral strips; legs marked with large spots; body ground color cream to light gray.

RANGE.—Lahontan Basin in western Nevada northwest into northeast California, north into southern Oregon, and northeast into the Snake River Valley of southwestern Idaho.

Crotaphytus wislizeni wislizeni
Baird and Girard

SPECIMENS EXAMINED.—Arizona, Yuma Co., CAS 33486, 34204-8 and 33490; SDNHM 16730 and 17123; MMZ 71080(4) and 71080(2). California, Imperial Co., BYU 41177; LACM 4007, 15649, and 37787-8; LBSC 1471-2; MMZ 122632(2); SDNHM 1879, 7143, 7847, 10937, 11346, 13352, 13911, 18596, 20967, 28762, 36541, and 39735. Inyo Co., CAS 65117, 65318-20, 65336, 65381, 65486-8, 65529-31, 65583-4, and 65634; LACM 26804-6, 36668-9, and 52876; SDNHM 2503 and 12243. Kern Co., CAS 21234; LACM 4013, 26803, 53883-4, 63807, 63809-10, and 94709; MVZ 26026 and 70372; SDNHM 5877, 6047, 15877, 19483-5, 37438, 40005, and 41803. Los Angeles Co., LACM 4009, 15628-30, 15631, 15632-33, 15634, 15635, 15636, 15637, 15638, 15639, 15640, 15641-2, 15643, 15644, 15645, 15646-7, 15710, 26802, 52878, and 52879; MVZ 873 and 19652-4. Mono Co., SDNHM 28941. Riverside Co., BYU 40941-3 and 40945; CAS 45369-70; LACM 4011, 15648, 22218-9, 26807-8, and 52880-82; SDNHM 4999-5000, 8040, 11344, 19486, 20700-3, 22352, 29448, 31428, 31906-7, 39747, 39850, and 41339. San Bernardino Co., BYU 3108 and 40942; CAS 43181-4; LACM 4012, 4014, 15653-61, 21646-49, and 52877; SDNHM 2489, 2498, 4408, 5875-6, 7798, 9013-5, 20887, 23636, 25344, 25641-2, 28939-40, 28942, 29660, 31453, 38889, and 41201. San Diego Co., LBSC 1473-4;LACM 15651-2; SDNHM 44, 8041, 9952, 11099, 11345, 18593-5, 22328, 23411, 24036, 29516, 33943, and 38418.

Nevada, Clark Co., BYU 460, 504, 556, and 1541-2; LACM 15681-95; MMZ 84941(2), 90699-01; SDNHM 7626-7, 31718, 38675, and 40655-7. Elko Co., CAS 40933. Esmeralda Co., CAS 37801. Lander Co., BYU 2918; MMZ 84945 and 91868. Lincoln Co., BYU 9816; CAS 37014-18 and 38019-23. Mineral Co., MMZ 84948 and 117360. Nye Co., BYU (Nevada Test Site including Mercury and Rock valleys and areas in and associated with Frenchman, Jackass, and Yucca Flats) 3037-51, 5084-7, 3093-98, 17276-9, 17308-22, 17944, 18969, 18984, 21740-55, 23620, 23966, 30083, 30085-7, 30121, 30539, 30546, 30589-90, 30595, 30608-9, 31425, 31810-14, 32571, 32632-4, 33571, 33609, 40127, and 41452-5; CAS 37017-8, 37512-3, 37688-92, 37996, and 38019-23; LACM 15696 and 26810; MMZ 84942(2), 34943(4), 34946, 84951, 84953-6, 84957(2), and 117336. White Pine Co., BYU 558.

Utah, Beaver Co., BYU 580, 4302, 11349-53, and 12001-2. Iron Co., BYU 478, 2371, 2374, 2376-7, and 2899; MMZ 59573, UU 1659. Juab Co., BYU 2731, 3020, 3027, 10244, 11295-6, and 12496; MMZ 91870(2). Millard Co., BYU 481, 580, 4308, 9099, 10179, 11354, and 14843-53; CAS 893-4, 1530-2, 38031, 85399-00, and 54151-2; MMZ 70553, 70554(6), 70555(14), 70556(2), 70557(2), 70558-60, 70561(2), 60562-3, 70564(3), 70565(4), 70566, 70567(5), 70568(2), 70569(3), 70570(3), 84950, and 91869; SDNHM 893-4, 1530-2, and 26399-02. UU 3298-01. Salt Lake Co., UU 18. Sevier Co., SDNHM 37960, 38315-6, 38244-50, 38328-31, 38381-2, 39016-8, 39191, 39397-9, and 40571-3. Tooele Co., BYU 480, 1555, 14688, and 14843-53; MMZ 69432(2), 69433-4, 69435(4), 69436-7, and 91823; SDNHM 22998, 24988-9, and 26399-402. Utah Co., BYU 483, 576, 1578, 1633, 2210-11, 8496, 12196, 14690-1, 16601, 21506, 22474, and 22835; UU 1-4, 2a, and 3563-7. Washington Co., BYU 515, 680, 1635, 8464, 11382, 23657, 31970-1, and 31972-8; CAS 54085-6; SDNHM 21078, 24993, and 25643.

Mexico: Baja California Norte, BYU 23336; CAS 57446 and 90256; Sonora, BYU 3175; CAS-SU 17049-50; SDNHM 38251-4, 38605-6, 38888, and 40601; USNM 146455.

Crotaphytus wislizeni maculosus subsp. nov.

Specimens examined.—California, Modoc Co., CAS 63912; LACM 4010. Idaho, Ada Co., CAS 41366-71, 45417-25, and 53781-3. Boise Co., MMZ 54072, 68245(2), 68246-8, and 93084(4). Bingham Co., CAS 41275-6. Butte Co., BYU 30773. Canyon Co., MMZ 68249. Elmore Co., MMZ 60250; SDNHM 1452. Owyhee Co., BYU 2835; CAS 55261, 64151-4, and 64161-2; MMZ 68251(2), 122787(2), 122790, and 125694.

Oregon, Harney Co., BYU 41445, 41454-71; Malheur Co., MMZ 124618(2).

Nevada, Churchill Co., MMZ 72653, 84944(2), and 84949; Humboldt Co., MMZ 43171-7, 60029, 77996, 85618(5), and 91865-7. Lyon Co., LACM 15696. Ormsby Co., SDNHM 38417. Pershing Co., MMZ 84947 and 91825(2). Washoe Co., CAS 38016-7, 40510-15, and 40527-32; MMZ 91824, 91826(2), 91827(2), and 91828-9.

Crotaphytus wislizeni silus Stejneger

Specimens examined.—Fresno Co., CAS 22713, 22716-8, 22857-8, 23212-3, 23250, 23271, 23292, and 85416; King Co., MVZ 116442; Kern Co., CAS 3046, 39000, 43266, and 47996; LACM 4008, 15662-9, 15671-6, 15679-80, and 26809; San Luis Obispo Co., CAS 32195, 23200, and 23203-4; MVZ 2751, 8817, and 61077. MVZ 2725, 2733, 2735, 2737-43, 2747, 2749, 3775-81, 4891-2, 4894-8, 6851, 43142, and 72353-4.

Specimens showing one or more intergrading characters with *C. w. wislizeni*: CAS 1243, 12787-8 (Frazier Park), 38999 (Tehachapi Mts.); LACM 15650 (Mt. Pinus), 15670 (25 mi S. Bakersfield), 15671 (Wheeler Ridge), 15677 (McKittrick), 52879 (Black Butte), 15630-3 (Lovejoy Sp.), 15635 (Piute Butte): MVZ 43139 (3 mi SW Kicks Corner).

MORPHOLOGY AND VARIATIONS

These attractive lizards of moderate size have only recently been critically examined. Since Smith (1946) noted the considerable variation in patterns, we have observed a correlation between color patterns and geographic distribution. Tanner and Banta (1963) described and figured the pattern for *C. w. wislizeni* in Arizona and New Mexico and for *C. w. punctatus* in the upper Colorado River Basin. Montanucci (1970) discussed in detail the color patterns of *C. w. silus* in the San Joaquin Valley of California. Although these and other studies have made some comparisons with those populations occurring in the Great Basin, a critical examination of a large series has not been made. It is hoped that this study will yield the results necessary to provide some conclusions for the leopard lizards of this large and varied area.

COLOR PATTERN TYPES

SPOTTING.—In the western United States and northern Mexico there are five distinct spotting patterns:

1. A pattern of moderately sized spots, with a circle of light spots surrounding the larger dark spots. This pattern is prominent

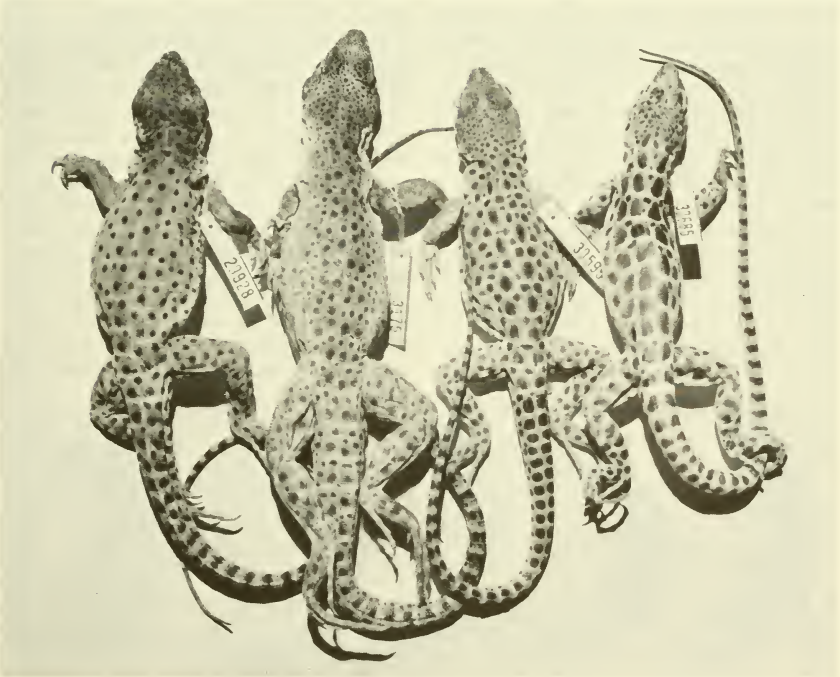

Fig. 4. Dorsal views of (a) *C. w. punctatus*, (b) *C. w. wislizeni*, (c) *C. wislizeni* NTS intergrade, (d) *C. w. maculosus*.

on the dorsal aspect of the trunk, base of the tail, and hind legs. There may also be smaller spots interspersed between the larger ones and on the lateral parts of the trunk and tail. The white transverse bars may or may not be apparent; when present they are more obvious posteriorly on the trunk and base of tail (Fig. 4b).

2. A pattern of small spots, widely dispersed on the trunk, tail, and legs. The background is lighter than in those with other patterns. Individuals with this pattern show no white dots in association with the small dark spots. Furthermore, there is a greater uniformity in the size of spots than in other patterns. The white bars are distinct but narrow and less prominent than in populations occurring west of the Colorado River (Fig. 4a).

3. A pattern of moderate to large spots, with light centers in juveniles but not in adults. The light center is apparently lost by a gradual darkening and blending with the ground color. As the blending of colors occurs, the spots are subdivided to form from two to four closely associated or slightly connected spots. This pattern is characteristic of *C. w. neseotes* from Cedros Island and many individuals from Baja California, Mexico.

4. A pattern in which the areas between the white transverse bars are from a solid dark brown to a nearly black color. In juveniles there are spots present, but these are lost in adults by a suffusion of dark pigment that obscures all spotting. The transverse white bars are distinct and much wider than in other patterns. This pattern occurs in the populations in the lower parts of the San Joaquin Valley. We note, however, that the spotted pattern of juvenile *C. w. silus* is very similar to that of adults from Antelope Valley (Fig. 5).

5. The subspecies *C. w. maculosus* has a pattern of large dark spots between the transverse white bars and a lighter continuous cycle around the larger spots. This is reminiscent of the pattern in *C. w. wislizeni* except for larger spots and a light circle rather than a series of small light spots. The transverse white bars are moderate in size, being narrower than in *C. w. silus* but wider than in *C. w. punctatus*. In some individuals the transverse bars become diffused and blended with the light circles, which produces an irregular netlike configuration of light markings (Fig. 4d).

Montanucci (1970) referred to those light dots, circles, and other additions to the spotted pattern as adornments. This is seemingly an appropriate way to treat all additions to the basic pattern of spots. Only a few populations are without adornments. Specimens of *C. w. punctatus* from southeastern Utah have a light ground color and small dark brown spots (Tanner and Banta 1963). Those from near Bakersfield, Kern County, and north in Fresno County, California, have as adults reduced the pattern to a uniform dark color between the light transverse bars, thus eliminating the basic spot pattern.

An examination of hatchlings and small juveniles demonstrates that *C. wislizeni* has

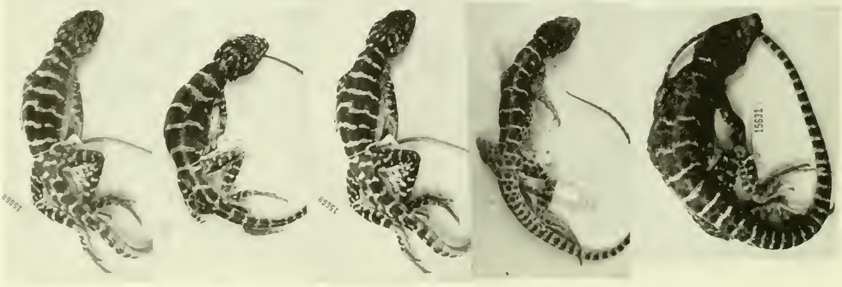

Fig. 5. Dorsal view of specimens of *C. w. silus* (A-C; D and E, intergrades, Antelope Valley). LACM tags.

throughout its wide range maintained a spotted pattern in its young. This juvenile pattern is modified in adults of all color pattern types. The similarity of hatchling patterns is unique, and we are impressed with this unifying character throughout the species. Adjacent populations with very different adult patterns such as Antelope Valley (Los Angeles County), with its spotted pattern and the dark nonspotted pattern in the Bakersfield population (Kern County), have similar spotted patterns in hatchlings and young juveniles. Populations occurring between those populations with patterns as described above (1-5) show many variants. This is most evident in populations occurring in southern Nevada, in which a series from valleys such as Frenchman Flat or Mercury may have individuals with patterns similar to all other populations except that pattern found in the San Joaquin Valley (Fig. 2). In patterns 3 and 5 the white transverse bars may be absent on all or part of the trunk or so intertwined with the light areas between the spots as to lose their identity.

SCALE PATTERNS

POSTMENTALS.—Only a few scale patterns vary noticeably within this species. As noted in Part I (Tanner and Banta 1963), the postmentals show significant variations between *C. w. wislizeni* and *C. w. punctatus*. We have reexamined this character in 101 specimens from the Upper Colorado River area of southeastern Utah and northeastern Arizona, and our findings indicate an average postmental count of 5.71 in contrast to the 5.72 reported by us in 1963 (Table 1). This figure includes a series from Kane County, Utah, which has a lower average (5.17), and we consider Kane County to be a lane of dispersal into southwestern Utah and eastern Nevada. If the specimens from Kane County are removed, the postmentals for *C. w. punctatus* average 5.81.

In Table 2 we have averaged the postmentals for Washington County, and for populations in the Great Basin of west central Utah, Nevada, California, Oregon, and in the Snake River Valley of southwestern Idaho. These figures show an average decrease in the numbers of postmentals from east to west. However, this decrease is accompanied by an increase in the range of variation. We consider this a strong indicator of intergradation, particularly in those populations occurring in Washington County, Utah, the Great Basin of west central Utah, at the Nevada Test Site, and in southern Nevada.

Those populations occurring along the northern limits of distribution (Table 2: Harney County, Oregon, and southwestern Idaho) show a noticeable increase in the number of postmentals when compared to other Great Basin populations. These same populations also show a decrease in the range of variation, with none of the Oregon

TABLE 1. Variation in the postmentals in populations occurring in northern Arizona and southeastern Utah.

Area	Number	Range	Mean
Utah Populations			
Grand County	34	4-7	5.7
Emery County	17	5-7	6.0
Garfield County	15	4-7	5.9
San Juan County	6	4-6	5.5
Northeast Arizona	6	4-7	5.8
Kane County	23	4-6	5.2
	101		5.71

TABLE 2. Variation in the postmentals in the Great Basin and adjacent areas in Utah, Nevada, Oregon, Idaho, and California.

Area	Number	Range	Mean
Washington County, Utah	15	4-5	4.5
Great Basin			
Western Utah	57	2-6	4.1
Nevada Test Site	56	2-7	4.2
Lahontan Basin	29	2-6	4.1
Harney County, Oregon	9	4-6	5.0
San Bernardino, Riverside County	77	2-6	4.2
Inyo County	23	2-6	4.4
Imperial County	21	3-6	4.4
Antelope Valley, Los Angeles County	31	2-6	4.4
Snake River Valley			
Southwest Idaho	34	3-6	4.6
	352		

specimens with less than four and only one Idaho specimen with three postmentals. Although our samples are small for some populations (Oregon), they show consistency except for Washington County, Utah, which we include with the large and varied intergrading populations occurring in southwestern Utah and much of central and southern Nevada. The increase in the number of postmentals for the northern populations of the subspecies *maculosus*, and for that matter *punctatus*, is not explainable except as a response to the climatic changes in the northern localities.

An examination of the scale pattern summaries in Table 3 indicates that there are only minor variations. A few trends are apparent, such as a higher range and average for femoral pores and the scale rows around the body in the populations of Baja California Sur, Mexico. In neither of these patterns does the lower limits of the range show as few pores or rows of scales as in other populations. Only in the higher averages, particularly in the scale rows, are the variations between the Baja California Sur and the continental populations obvious. In all populations and subspecies there is an overlapping in the ranges of all scale patterns examined. In most patterns this overlapping is extensive.

The Nevada Test Site population shows greater variation than other adjoining populations in the number of scale rows, ventrals, and postmentals. In the scale rows the average is low, with only *C. w. punctatus* lower. The ventrals average the lowest of all populations studied, and the range for the postmentals from two to seven is greater than in other populations.

SKULL MEASUREMENTS

SKULL LENGTH/WIDTH RATIO.— The ratio of the skull width into its length (Fig. 6) substantiates the data presented by Montanucci (1970) that the skull is shorter in the San Joaquin population (*silus*) than other subspecies and populations. There is, however, an overlapping with other populations of approximately 25 to 50 percent when compared with other populations examined (Fig. 6).

DISCUSSION

On the basis of color and color pattern, we must assume that *C. wislizeni* expanded

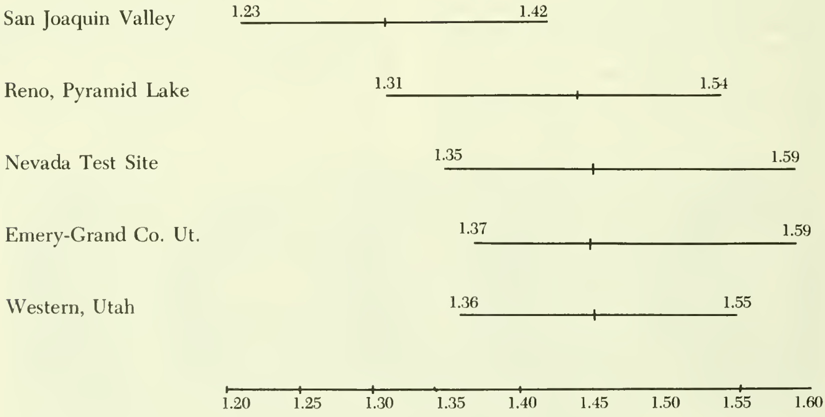

Fig. 6. Ratio of width into skull length (from rostral to median posterior of skull). Specimens used and data available on request.

TABLE 3. Scale patterns in subspecies or populations of *Crotaphytus wislizeni* (mean in parenthesis).

Subspecies or population	Total femoral pores	Total supralabials	Total infralabials	Scale rows	Dorsals	Ventrals	Post-mentals
C. w. neseotes	37-59(45.9)	26-32(27.9)	24-30(27.4)	♂ 186-202(193.5) ♀ 185-207(199.7)	180-206(194.5) 191-208(200.6)	86-101(92.4) 91-105(96.6)	2-4(3.6)
C. w. copei	38-54(46.2)	27-32(29.5)	26-33(29.9)	184-212(196.4)	175-227(200.7)	86-110(95.6)	2-6(4.0)
C. w. wislizeni							
1. Arizona, New Mexico, Texas, Chihuahua, and Sonora	34-50(42.1)	24-34(28.8)	24-33(28.3)	176-200(183)	174-231(205.6)	95-112(106.2)	2-6(3.7)
2. S. Nevada and S. California	36-55(43.8)	26-37(30.8)	24-35(29.6)	164-214(191.2)	170.-245(213.1)	85-118(101.0)	2.6(4.3)
3. SW. Utah Great Basin and E. Nevada	31-47(38.0)	22-37(28.4)	21-30(25.4)	154-190(182.0)	180-217(196.5)	84-116(96.0)	2-6(4.0)
4. Nevada Test Site	35-45(39.9)	24-36(30.0)	22-33(27.5)	148-198(171.8)	172-210(194.0)	72-102(87.1)	2-7(4.1)
C. w. maculosus	34-47(39.95)	25-39(30.1)	25-34(29.2)	165-192(179.0)	175-212(193.4)	87-114(95.7)	3-6(4.45)
C. w. punctatus	35-52(42.35)	25-36(29.6)	24-35(29.1)	145-181(164.7)	178-215(199.2)	85-121(101.2)	4-7(5.7)

its range rapidly at the close of the Pleistocene and occupied the low valleys in southern New Mexico, southern Arizona, northern Sonora, and southern California, perhaps before entering the areas of the high plateaus. Such an hypothesis would have much of southern California, southern Nevada, and the low valleys along the California-Nevada line occupied before the invasion of *C. w. punctatus* occurred in western Utah and east central Nevada. This hypothesis is based on the fact that color patterns in southern California, the Antelope and San Joaquin valleys of California, and the populations in northern Nevada (*maculosus*) do not seem to be in any way similar or related to the *punctatus* pattern. The invasion of western Utah and southeastern Nevada by *punctatus* seems to have occurred more recently. This is based on the fact that there is a real jumbling of pattern in southern Nevada (NTS); and from this general area a diminishing effect is seen as one examines specimens from the southwest and north. To the northeast, that is from southern Nevada to Washington County, Utah, the influence of *punctatus* increases. If populations of *wislizeni* had occupied these areas before *punctatus* arrived, they have or are in the process of a continuing and extensive introgression with a strong *punctatus* influence. This is most obvious throughout southern and extreme eastern Nevada.

There is reason to suspect that the mainflow of leopard lizard migration at the close of the Pleistocene was from southern California, through the low valleys of eastern California north into the Lahontan Basin of west central Nevada. As the higher valleys of western Utah and eastern Nevada became environmentally available, they were occupied. Furthermore, with improving climatic conditions, the terrain (with its north-south-oriented mountains) is well suited for a rapid movement to the north (or south) through the broad alluvial valleys.

Migration into the Bonneville Basin of western Utah and the high valleys of central and eastern Nevada was slower. Elevation barriers ranging up to 5,000 feet may have remained cool and were probably most responsible for slowing the northward movement. This is still effective for some species such as *Sceloporus magister* and *Callisaurus ventralis*, which are not in the Bonneville Basin but have reached the Lahontan Basin. The early arrival and partial isolation in the Lahontan Basin provided a greater opportunity for differentiation and also time to extend their ranges into southern Oregon, northeastern California, and southwestern Idaho. Although those populations now in the Bonneville Basin are partially isolated, they appear to have been derived too soon to have differentiated as much as those occupying the Lahontan Basin.

In western Utah, southern Nevada, and adjoining California (San Bernardino and Inyo counties) there is a large area of intergradation between those populations existing in the area or those that moved north from southern California (*C. w. wislizeni*) and those moving into the area from southeastern Utah and northern Arizona (*C. w. punctatus*). Because of the size of the area of intergradation, one may assume that the gene flow from these populations has been strong and steady. As one samples populations radiating from this central area, the populations are more homogeneous. The one area of intergradation most difficult to interpret is the populations in the Bonneville Basin of western Utah and eastern Nevada. Within this basin (from Iron County to Box Elder County, Utah) the populations are more homologous than those from the Nevada Test Site, but they still provide an occasional individual with either a *wislizeni* or a *punctatus* pattern.

Apparently, introgression had occurred before the Bonneville Basin was occupied, or there was a mingling of the two as they moved northward at about the same time. Once movement was slowed and population stability was achieved, differentiation occurred. This is seen in such populations as those in the Lahontan Basin and San Joaquin Valley, and to an extent in Antelope Valley (Los Angeles County) and the Coachella Valley. Differentiation has occurred primarily on the fringes of distribution, with the large central area in southwestern Utah, southern Nevada, and much of southeastern California occupied by a population with variable degrees of intergrading characteristics.

Perhaps the most difficult populations to understand occur in the areas of western San Bernardino County (west of Barstow), eastern Kern County (near Mojave), and northern Los Angeles County (Palmdale-Lancaster area). Populations in these areas are far enough removed from the intergrading population of southern Nevada to reflect some pattern characteristics of their own. This is particularly true for Antelope Valley in northern Los Angeles County, where a darker ground color obtains and the spots are darker and more uniform in size and color. Although our samples are small, those seen reflect a slow but steady change from *C. w. wislizeni* to *C. w. silus* from western San Bernardino County through Antelope Valley to the areas near Fraser Park and on westward into the low hills and valleys of northern Ventura and Santa Barbara counties.

The data concerning *C. w. silus* presented by Montanucci (1970) agrees generally with our findings. Any differences are in the area of interpretation. We see in adjoining populations (Antelope Valley, Los Angeles County, and those near Weldon, San Bernardino County) strong influences of the adult and juvenile color patterns of *C. w. silus*. We also recognize a more sudden change in pattern from the foothills surrounding the San Joaquin Valley to the valley floor.

In other areas of the extensive leopard lizard range ecological changes are more gradual, or they occur in smaller geographical areas which do not seemingly provide sufficient space for isolation and thus slowly induce genetic adaptive change. This gradual change in the environment has provided for wide areas of introgression in much of the Great Basin and is perhaps unique in that the central area of distribution (southern and eastern Nevada, southern California, and western Utah) represents a large area of genetic variation as deduced from the phenotype. As indicated above, within this wide area of diversity subspecific patterns (except for *silus*, *copei*, and *neseotes*) appear in some individuals. Within the populations considerable individual variation occurs and is so extensive in some areas that few lizards show the same phenotypic pattern. Only in the fringe areas where some degree of isolation obtains do we find subspecies or incipient subspecies.

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SYZYGIOXYLON CHHINDWARENSE, A NEW FOSSIL WOOD FROM THE DECCAN INTERTRAPPEAN SERIES OF INDIA

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Abstract.— A petrified wood related to genera of the family Myrtaceae was collected from the Deccan Intertrappean Series of India. On comparison with fossil woods of this family, it most closely resembles *Syzygioxylon* Ingle (1973). The specimen differs from described species of *Syzygioxylon* and, therefore, it is proposed as the new species *Syzygioxylon chhindwarense*.

Fossil wood resembling species of *Eugenia* (Myrtaceae) has been collected from a black chert in the Deccan Intertrappean beds near the Mohgaon Kalan locality in Chhindwara District, Madhya Pradesh, India. Myrtaceous woods have been described previously from these formations by Ingle (1973) and Patil and Singh (1974). Prakash (1965) reviewed reports on dicotyledonous woods from India and the Far East which included those from this locality. Since then, additional fossil woods from the Mohgaon Kalan locality have been described by Chitaley and Patel (1971), Chitaley and Patil (1972), Chitaley and Kate (1972), and Nambudiri and Tidwell (1975).

Description

The specimen is 37 mm in diameter and consists of secondary xylem. The xylem is diffuse porous, and two growth rings are faintly visible to the unaided eye. Vessels are numerous, small, and faintly visible to the unaided eye, although they are distinct under a hand lens. They are round to oval, with a tangential diameter of 77.5 μm to 116 μm and a radial diameter of 145 μm to 164 μm. They are mostly solitary, occasionally in pairs and rarely in radial multiples of 2 to 4 vessels (Figs. 1a, 2a). Distribution of these vessels is 85 per sq cm. They have simple, oblique perforation plates (Fig. 1b). The vessel wall is 2.5 μm in thickness. Intervascular pit pairs are round to oval, alternate, and vestured (Fig. 1d). They have a mean diameter of 4.2 μm.

Parenchyma is paratracheal, either scanty or vasicentric (Fig. 2b). Generally, they form one or two layers around the vessels. These are 41 μm long and 7 μm broad. Vessel to parenchyma pits were not observed.

Rays (Fig. 1c) are extremely fine to moderately fine, faintly visible to the unaided eye. They are heterogeneous and uniseriate as well as 2-4 seriate. Some of the multiseriate rays are fused by their tips. Uniseriate rays range from 68 μm to 240 μm long. Multiseriate rays are from 435 μm to 659 μm in length. The former has a mean width of 9 μm, whereas the latter are 30 μm in width.

Vessel to ray pits (crossfield pitting) are similar to intervascular pit pairs (Fig. 2d).

Fibres are libriform and nonlibriform and thin walled. They are 388 μm long and 14 μm broad. Fibres are polygonal in cross section and are septate as well as nonseptate (Fig. 2c).

Discussion

The fossil wood of *Syzygioxylon chhindwarense* is similar to members of the Ochnaceae, Sonneratiaceae, Vochysiaceae, Punicaceae, Dipterocarpaceae, and Myrtaceae families. Wood of Ochnaceae plants with very scanty parenchyma differ from the occasional occurrence of the vasicentric type in the present wood. The aliform confluent parenchyma in genera of the Vochysiaceae separates the xylem of this family from S. *chhindwarense*. The xylem of Sonneratiaceae has exclusively uniseriate rays. Xylem of punicaceous genera lacks parenchyma, whereas woods of Dipterocarpaceae contains apotracheal parenchyma rather than the paratracheal type of S. *chhindwarense*. Thus our specimen differs from these families. However, it is similar to several taxa of the Myrtaceae. The paratracheal scanty or vasicentric parenchyma, as observed in the present wood, is contained in the myrtaceous genera *Eucalyptus*, *Gonidesia*, *Xanthostemon*, and *Eugenia*. In contrast, vessel multiples are fewer in S. *chhindwarense* than in *Eucalyptus*. Rays of *Gonidesia* and *Xanthostemon* differ from those of our specimen. They are up to 8 cells wide in *Gonidesia* and from 4 to 6 cells wide in *Xanthostemon*. *Eugenia* is, therefore, the closest extant genus to S. *chhindwarense*.

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Vessel arrangement, nature of the intervascular pit pairs, and type of rays in *Eugenia* correspond to that of the present wood. *Eugenia* Linn. is one of the largest genera of tropical plants, with about 1000 species—of which some 150 are represented in the lowlands and mountains of the Malaysian Peninsula (Desch 1954) and four are commercial timbers of India (Pearson and Brown 1932). The common name for this genus is Kelat in Malaysia and Makaasin in the Philippines. Species of *Eugenia* range in size from dwarfed and shrubby treelets of the mountain tops to the medium-sized or quite large trees in the lowland forests. The anatomical structure of the wood of *Eugenia* is similar, but there is an appreciable variation in the amount and, to some degree, the distribution of wood parenchyma in different species. Some species of *Eugenia* have apotracheal parenchyma, whereas in others it is aliform confluent. In *Eugenia nitidula* Ridl., as in other species of this genus, the parenchyma is paratracheal vasicentric and only occasionally confluent. Thus no one species is entirely like our specimen. Other similar species are *E. longiflora* (Presl.) Vill., *E. polyantha* Wight, *E. rhamphiphylla* Craib, and *E. tetraptera* var. *pseudotetraptera* Herd.

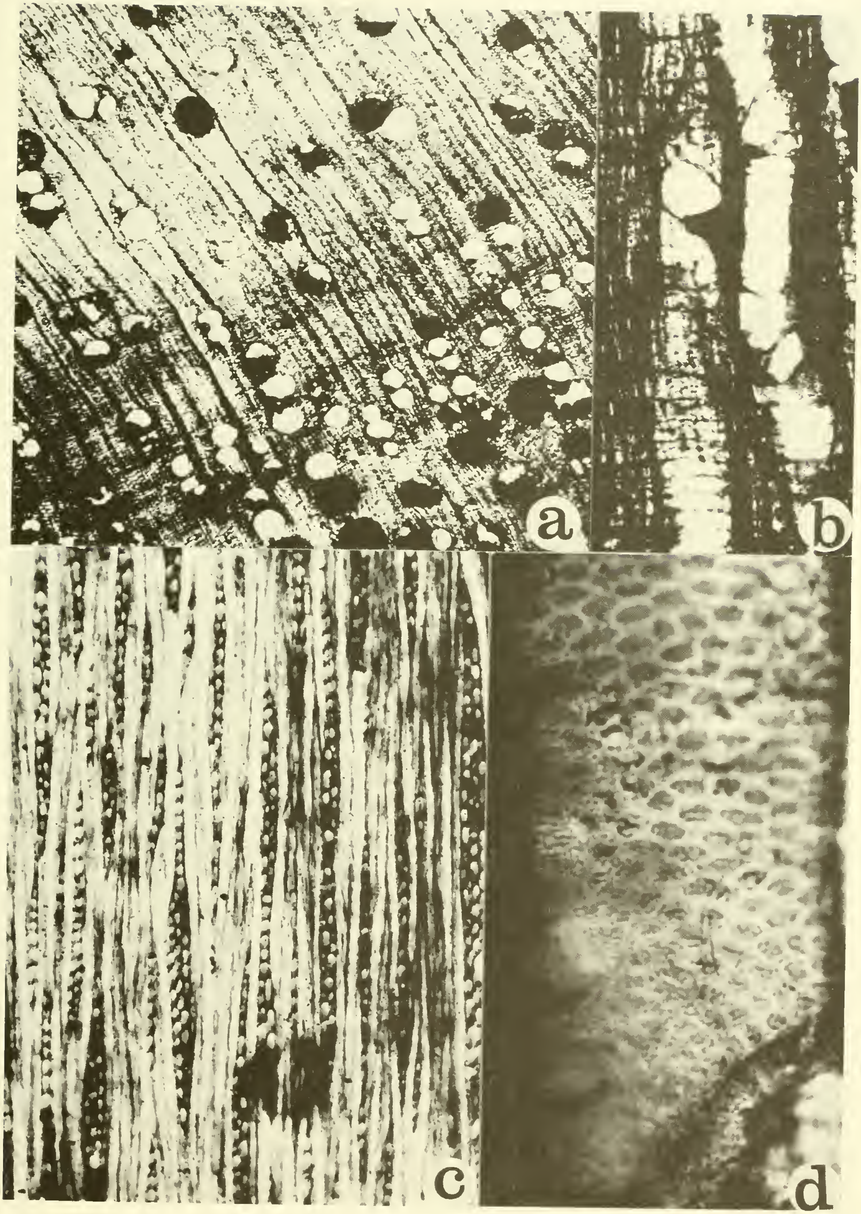
S. *chhindwarense* varies from the above mainly in its parenchyma distribution. It lacks either the confluent or aliform parenchyma that is present in the others. However, it is similar in having more distinct growth rings, which also occur in *E. cumingiana* Vidal and *E. rhamphiphylla*. This feature stands out because one characteristic of the genus is the general lack or inconspicuous nature of the growth rings. Two features that are often present in some species of *Eugenia* but lacking in our fossil form are frequent tyloses and traumatic gum ducts, the latter occurring horizontally in the rays of some species of *Eugenia*.

The present wood demonstrates closest affinities to described species of the fossil genus *Syzygioxylon* Ingle. However, there are sufficient differences between them and our specimen to propose ours as the new species, *Syzygioxylon chhindwarense*.

Ingle (1973) described *Syzygioxylon mandlaense* from the Mandla District in Madhya Pradesh, India. This species shows both paratracheal and metatracheal parenchyma, a condition differentiating it from the present specimen. In proposing *Syzygioxylon* as a new genus, Ingle (1973) demonstrated similarities between the living genus *Syzygium* and his taxon. However, many species of *Syzygium* with which he compared his specimen have been placed in *Eugenia* by Pearson and Brown (1932).

From the Mohgaon Kalan locality, Patil and Singh (1974) reported *Syzygioxylon mohgaoense*. This species has metatracheal parenchyma along with the paratracheal vasicentric type. In S. *mohgaoense* the vasicentric parenchyma becomes aliform. Kramer (1974) described a myrtaceous wood from the Tertiary beds of Java under the name *Syzygioxylon bataviae*. However, he

Fig. 1. *Syzygioxylon chhindwarense* sp. nov.: a) Transverse section illustrating vessel distribution (X45). b) Vessels with simple perforation plates (X50). c) Tangential section showing narrow rays (X110). d) Vessel exhibiting alternating, vestured intervascular pitting (X900).


a
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d

was not aware of the institution of the genus *Syzygioxylon* by Ingle (1973) and treated *Syzygioxylon* as a new genus in his paper (Kramer 1974). *Syzygioxylon bataviae* has paratracheal aliform parenchyma. The short lateral extensions of the aliform parenchyma in this species unite and form discontinuous confluent strands.

Regardless of these differences, S. *chhindwarense* shows resemblances to S. *mandlaense* Ingle (1973) and S. *bataviae* Kramer (1974). The similarities are in the arrangement of vessels and in the septate and nonseptate fibres. However, the wood is closer to S. *mohgaoense* Patil and Singh (1974) than to the other two species. The characteristics common to S. *mohgaoense* and S. *chhindwarense* are the nature and arrangement of vessels, some united rays, and the septate or nonseptate fibres. However, they differ from each other in the total absence of metatracheal diffuse parenchyma and the presence of vestured pits in the present specimen. Shallom (1960) described a similar fossil wood, *Barringtonioxylon deccanense*, from the Intertrappean beds of Mahurzari. She assigned it to the family Lecythidaceae, whereas Chowdhury (1965) considered it to be a member of the Myrtaceae. However, Chowdhury (1965) suggested that *B. deccanense* be reinvestigated.

Myrtaceae is probably the oldest representative of Myrtales (Muller 1970) and possibly extended back into Cenomanian time (Penny 1969). From the Eocene Green River Formation of northwestern Colorado and northeastern Utah, MacGinite (1969) reported a leaf impression *Eugenia americana*. *E. arenaceaformis* was described earlier from the Oligocene Florissant flora of Colorado (MacGinite 1953). Myrtaceous fossils are also known from Eocene of Europe (Krutzsch 1967) and Cretaceous of Argentina (Menendez 1972). The family is estimated to contain over 70 genera and about 2,800 species of trees and shrubs, widely distributed throughout the tropical and subtropical regions of the world. Members of this family occur especially in the hot zones of low rainfall bordering on the tropics rather than in the rain forest belt (Desch 1954). Raven and Axelrod (1974) noted that they are abundant in tropical Asia, South America, and Australia.

Several researchers (Dadswell and Ingle 1947, Pike 1956, Chattaway 1959, Schmid 1972) have studied the taxonomic problem of *Eugenia* and *Syzygium*. They, generally, followed Merril and Perry (1938) in suggesting that genus *Eugenia* be restricted to species of the New World and *Syzygium* be utilized for the majority of species of this taxon in the Old World.

In comparing the fossil species of *Syzygioxylon* with the criteria used by Dadswell and Ingle (1947) for separating *Eugenia* and *Syzygium*, two species (S. *chhindwarense* and S. *mandlaense*) have more characters in common with *Eugenia* than *Syzygium*. This is interesting considering that their collection localities are in the Old World and not the New. This paradox can be partially explained by speculating upon the origin of *Eugenia* and *Syzygium*. The origin of these two genera may have been from a common ancestor such as *Syzygioxylon*.

DIAGNOSIS OF SPECIES

Syzygioxylon chhindwarense, nov. sp., wood diffuse porous, two growth rings faintly visible; vessels numerous; solitary, in pairs or in radial multiples of 2 to 4; tangenial diameter 77.5 μm to 116 μm radial diameter, 145 μm to 164 μm, vessel wall 2.5 μm thick; perforation simple, plates obliquely placed; intervascular pit pairs round to oval, alternate, 4.2 μm in diameter, vestured; parenchyma paratracheal, vasicentric or scanty; rays extremely to moderately fine, uniseriate rays 68 μm to 240 μm long and 9 μm broad, multiseriate rays 435 μm to 659 μm in length and 30 μm in width; vessel ray pits similar to intervascular pit pairs; fibres libriform and nonlibriform, mostly aseptate but few septate, 388 μm long and 14 μm broad, polygonal in cross view.

HOLOTYPE.—MOG 69/N (To be deposited at the Birbal Sahni Institute of Palaeobotany, Lucknow, India.)

Locality.— Mohgaon Kalan

Horizon.— Deccan Intertrappean Series

Age.— Early Eocene

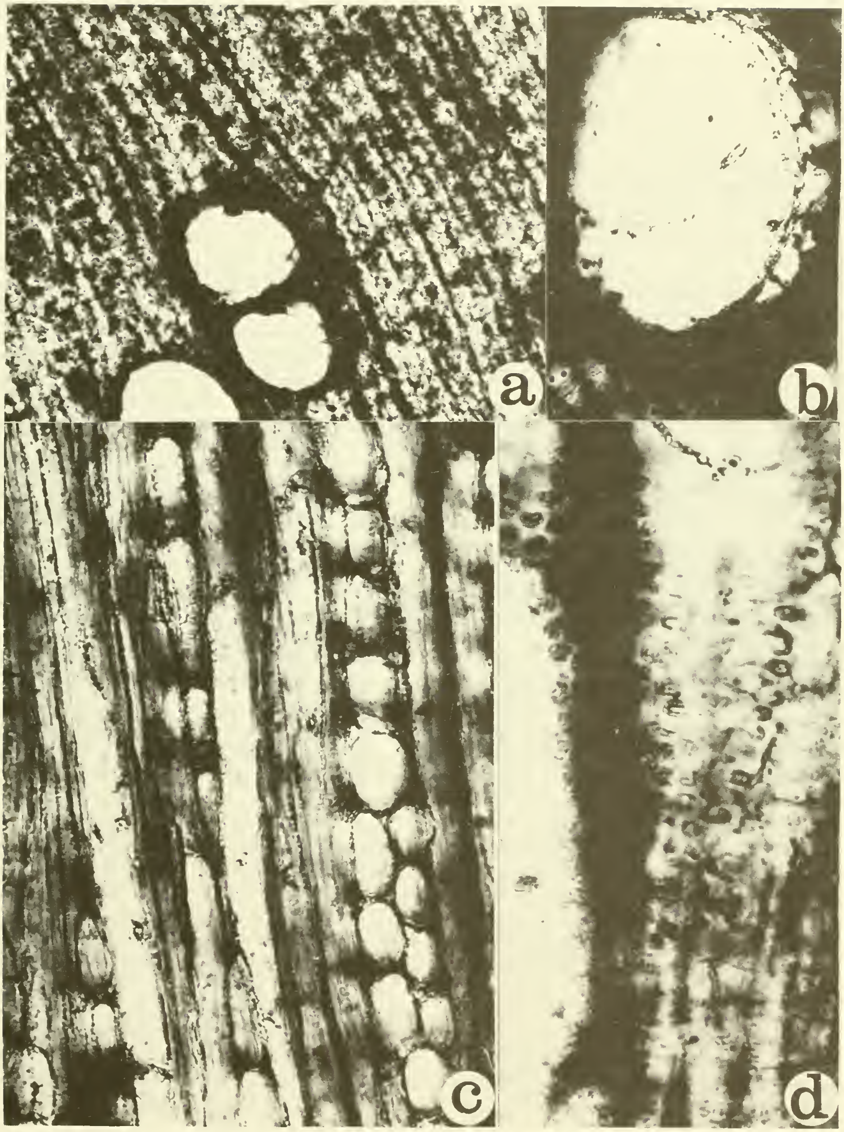

Fig. 2. *Syzygioxylon chhindwarense* sp. nov.: a) Close up of radial multiple of two vessels (X145). b) Vessel in transverse section with vasicentric parenchyma (X340). c) Tangential section showing nonseptate fibres (X450). d) Vessel to ray pits (crossfield pitting) on vessel. Note their similarity to the intervascular pitting (X620) (See Fig. 1d).

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BIRDS OF GUNNISON AND CUB ISLANDS GREAT SALT LAKE, UTAH

F. L. Knopf[1] and V. C. Bachman[2]

Abstract.— A total of 87 avian species were recorded on islands of Great Salt Lake by Behle, with 17 observed on Gunnison and Cub islands. This paper presents sightings and salvaged carcasses recorded on Gunnison and Cub islands, 1972-1974. Of the 112 species observed, 95 are first records for Gunnison and Cub islands and 49 are first records on or near any island of Great Salt Lake. Over 90 percent of species observed on the islands were transients.

Behle (1958) reported a total of 87 avian species occurring on the islands of Great Salt Lake, Utah. Those records resulted from collecting expeditions to larger islands, plus field observations of species during brief visits to smaller islands. This paper reports observations of species recorded during prolonged stays on two of the smaller islands, 1972-1974.

Nine islands occur within Great Salt Lake (for map, see Marshall 1940). Gunnison and Cub islands lie about 25 m apart in the northwest arm of the lake, approximately 14 km north of Lakeside, Utah, 40 km from Promontory Point and 13 km from the west shoreline. Water depths around the islands average 3 m, and these plus the distance to the western shoreline vary with annual fluctuations in water levels of the lake (Knopf 1974). The two islands become a single land mass during years when the lake level drops approximately one meter below the "normal" of 1,280 m above sea level.

Gunnison Island is about 1.6 km long by 0.8 km wide with its long axis extending in a north-south direcion. This island has an irregular shoreline of 4.5 km with four small bay areas, rises 85 m above mean lake level, and includes 66 ha. The substrate is loose soil with protruding rocks and cliffs. The shorelines are rock except for sandy areas along the bays. Vegetation is typical of the Great Basin desert, with June Grass (*Bromus tectorum*) predominating. *Opuntia fragilis*, *Salsola kali*, and *Bassia hyssopifolia* are also widely dispersed and common. Sandy areas along the shoreline support pure or mixed stands of *Sarcobatus vermiculatus*, *Atriplex* sp., and *Chrysothamnus nauseosus*, with the latter also occurring on north- and east-facing slopes at higher elevations.

Cub Island lies just north and east of Gunnison, is comma shaped, and comprises 3.2 ha. The physiography, substrate, and vegetation of Cub are similar to Gunnison, although larger vegetative forms are less common. *Sarcobatus* is absent. This latter species was used by many transient birds (Tyrannidae, Sylviidae) on Gunnison Island, birds not seen elsewhere on the islands. The nearest fresh water is at Locomotive Springs, about 40 km north of the islands.

Sightings of birds were recorded between 15 April and 4 August 1972; 6 April and 2 August 1973; and 5 April and 25 July 1974. We spent 11 days on the islands in 1972, and over 70 days each in 1973 and 1974. We surveyed the islands for birds at least one hour daily and also recorded all sightings of species observed at other times. Each sighting reported herein was verified at the time of the observation by at least one other person. The specific area surveyed included the islands plus the lake surface within 25 m of shoreline.

List of species

Behle (1958) lists 17 species of birds reported on Gunnison Island, with no separate account for Cub Island. We recorded 15 of those species from 1972 to 1974 also. The following list (a preliminary listing was reported in Rawley 1976) includes the dates of sight records for 95 additional species (denoted by * or **), giving a total of 112 species recorded on Gunnison and Cub islands. In addition, 47 of the species (denoted by ** only) observed in these efforts represent new records for any island in Great Salt Lake, bringing the total to 134 species occurring on all islands. Carcasses of Great Egret (*Casmerodius albus*) and Ancient Murrelet (*Synthliboramphus antiquus*) found on Gunnison Island may have washed ashore after death and have not been included in the Gunnison/Cub Island list. They do represent species recorded for the first time for Great Salt Lake, bringing the lake total to 136, (49 new records in this paper). For information on the murrelet, see Knopf (1976).

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***Podiceps nigricollis*. Eared Grebe. 8 June 1973, flock of 25 birds 29-30 April 1974. Abundant on lake in migration.

***Aechmophorus occidentalis*. Western Grebe. 14 April 1974. Common on lake in migration.

Pelecanus erythrorhynchos. White Pelican. Nesting and abundant (Behle 1958), with 5,000 to 5,200 birds estimated for each season, 1972-1974 (Knopf 1975).

**Phalacrocorax auritus*. Double-crested Cormorant. 16 April 1972, 15 April 1974.

Ardea herodias. Great Blue Heron. Formally nesting on Gunnison Island (Behle 1958). One pair nested on Cub Island each season 1972-1974.

**Botaurus lentiginosus*. American Bittern. 14 May 1973.

**Plegadis chihi*. White-faced Ibis. Flock of 3 birds 16 May 1973.

**Branta canadensis*. Canada Goose. 24 April 1972, 14 April 1974, 6 May 1974.

**Anas acuta*. Pintail. Flock of 11 birds 29 May 1973.

**Anas crecca*. American Green-winged Teal. 15 April 1972, 6 April 1973.

***Anas discors*. Blue-winged Teal. 14 May 1973.

***Anas cyanoptera*. Cinnamon Teal. 23 April 1973, 15 May 1973, 14 April 1974.

***Anas americana*. American Wigeon. 1 May 1974, 3 birds in one flock.

***Melanitta deglandi*. White-winged Scoter. Two birds flew across Gunnison Island 15 April 1972.

***Oxyura jamaicensis*. Ruddy Duck. 14, 18 May 1973; 9, 15 May 1974.

***Mergus serrator*. Red-breasted Merganser. 16 April 1974.

***Cathartes aura*. Turkey Vulture. 23 May 1973.

***Accipiter gentilis*. Goshawk. 25 April 1973.

***Accipiter cooperii*. Cooper's Hawk. Two birds on Gunnison Island 6-7 May 1974.

Buteo swainsoni. Swainson's Hawk. 11 June 1948 (Behle 1949), 9 June 1974.

**Aquila chrysaetos*. Golden Eagle. 21 May 1974.

**Circus cyaneus*. Marsh Hawk. 4 August 1972, 6 April 1973, 15 May 1973, 24 July 1974.

Falco mexicanus. Prairie Falcon. One pair successfully nested on cliffs at the north end of Gunnison Island each year, 1972-1974. The species has apparently nested at the site annually since 1944 (Behle 1958).

***Falco columbarius*. Pigeon Hawk. 6 May 1973.

**Falco sparverius*. American Kestrel. 26 April 1972, 24 July 1974.

***Fulica americana*. American Coot. 4, 23 April 1973, 14 May 1973.

**Charadrius vociferus*. Killdeer. 4, 7 May 1973, 15 April 1974.

**Pluvialis squatarola*. Black-bellied Plover. 23-25 April 1973.

***Capella gallinago*. Common Snipe. 23 April 1973, 4 May 1973.

**Numenius americanus*. Long-billed Curlew. 20 April 1972, 3 May 1973.

***Tringa macularia*. Spotted Sandpiper. 6, 15-16 May 1973; 22-23 May 1974.

**Catoptrophorus semipalmatus*. Willet. 3, 8 May 1974. A total of 10 birds in 3 flocks.

***Calidris bairdii*. Baird's Sandpiper. 15 May 1973. A total of 26 individuals in a mixed flock with *Calidris pusilla*.

°°*Calidris pusilla*. Semipalmated Sandpiper. 15 May 1973, 3 individuals.

°°*Limosa fedoa*. Marbled Godwit. 3 May 1974 and 24 July 1974, a total of 36 individuals.

°*Recurvirostra americana*. American Avocet. 16 April 1974.

Himantopus mexicanus. Black-necked Stilt. Previously recorded on Gunnison Island (Behle 1958). Twenty-eight individuals seen in one flock 6 May 1974.

°*Phalaropus tricolor*. Wilson's Phalarope. 20 June 1973.

Larus californicus. California Gull. Gunnison Island is a traditional nesting site for California Gulls (Behle 1958). Numbers of the birds were estimated to be about 15,000 individuals annually, 1972-1974.

°°*Larus pipixcan*. Franklin's Gull. 4 May 1973.

°*Sterna caspia*. Caspian Tern. A single Caspian Tern "mobbed" investigators on Gunnison Island 4 August 1972. A nest was not located. Four nests (with incomplete clutches) were discovered at the same location 10 June 1974. A fifth nest was also observed 11 June 1974.

°°*Columba livia*. Rock Dove. 5 May 1973.

°*Zenaida macroura*. Mourning Dove. Late April through mid June annually. No nests were located.

Asio flammeus. Short-eared Owl. Permanent resident of Gunnison Island (Behle 1958). This species was present 1972–1974, with as many as 4 individuals being seen simultaneously. One investigator was harassed on Gunnison Island 20 May 1974 by a single bird, but no nest was found.

°°*Selasphorus platycercus*. Broad-tailed Hummingbird. 4, 14, 16 May 1973; 1, 23 May 1974.

°*Megaceryle alcyon*. Belted Kingfisher. 23 April 1973.

°*Colaptes auratus*. Common Flicker. 6 April 1973.

°°*Tyrannus verticalis*. Western Kingbird. 2 May 1974.

°°*Tyrannus vociferans*. Cassin's Kingbird. 5 May 1973. This is the northernmost record of the Cassin's Kingbird in Utah.

Myiarchus cinerascens. Ash-throated Flycatcher. 11 June 1949 (Behle 1958), 8, 22 May 1974.

Sayornis saya. Say's Phoebe. 11 June 1949 (Behle 1958), 6 May 1974.

°°*Empidonax hammondii*. Hammond's Flycatcher. 1 May 1974. This bird was considered *E. hammondii* based upon the contrast between yellowish underparts and a grayish crest, by olive-colored tinge on the back, and by tail-flicking behavior while perched. However, no definite means of discerning between *E. hammondii* and *E. oberholseri* is reliable in the field, and the classifying of this sighting as *hammondii* must be considered speculative.

Empidonax oberholseri. Dusky Flycatcher. This species was reported 8 June 1937 (Marshall and Leatham 1942), but its identity was questioned by Behle (1958). This species failed to appear in Rawley (1976) and was incorrectly listed as not observed on Gunnison or Cub Island. No sightings were available 1972-1974.

°°*Empidonax wrightii*. Gray Flycatcher. 14 May 1973; 15, 21 May 1974.

°°*Empidonax difficilis*. Western Flycatcher. 22-23, 28 May 1974.

°*Contopus sordidulus*. Western Wood Pewee. 4-14 May 1973, 14-22 May 1974.

°*Eremophilus alpestris*. Horned Lark. 23 April 1973, a flock of 8 individuals.

°°*Tachycineta thalassina*. Violet-green Swallow. 1 May 1974.

°°*Tachycineta bicolor*. Tree Swallow. 6 April 1973, 14 May 1974.

°°*Riparia riparia*. Bank Swallow. 1 May 1974.

°°*Stelgidopteryx ruficollis*. Rough-winged Swallow. 22 May 1974.

°*Hirundo rustica*. Barn Swallow. 25 April 1973; 5-6 May 1973; 1, 8-10, 15, 22 May 1974.

°°*Petrochelidon pyrrhonota*. Cliff Swallow. 25 April 1973, 10 May 1974.

Corvus corax. Common Raven. A common nesting species (Behle 1958). One pair nested annually 1972-1974.

°*Corvus brachyrhynchos*. Common Crow.

16 April 1972.

°°*Gymnorhinus cyanocephalus*. Pinon Jay. 15 May 1974, a single flock of 24 birds.

°°*Parus gambeli*. Mountain Chickadee. 22 May 1974, 3 individuals were seen in one flock in *Atriplex* bushes.

°°*Cinclus mexicanus*. Dipper. 12 May 1972, a lone bird sitting among rocks and in apparent good health.

Salpinctes obsoletus. Rock Wren. Nesting and abundant (Behle 1958), 1972-1974.

°*Mimus polyglottis*. Mockingbird. 28 May 1974.

°*Dumetella carolinensis*. Gray Catbird. 23 April 1973.

°*Oreoscoptes montanus*. Sage Thrasher. 30 April 1974; 6, 15, 28 May 1974; 11 June 1974.

°*Turdus migratorius*. American Robin. 23 April 1973, 4 May 1973, 29 April 1974, 2 May 1974.

°*Catharus guttatus*. Hermit Thrush. 4-5, 8, 14 May 1973; 29 April 1974; 2 May 1974.

°°*Catharus ustulatus*. Swainson's Thrush. 16 April 1972; 15, 22 May 1974.

°°*Myadestes townsendi*. Townsend's Solitaire. 6 May 1973.

°*Polioptila caerulea*. Blue-gray Gnatcatcher. 12 April 1973; 5-6 May 1973; 29 April 1974; 7, 21 May 1974.

°°*Regulus calendula*. Ruby-crowned Kinglet. 15 April 1972; 4, 8, 14 May 1973; 1-2, 8, 15 May 1974.

°°*Anthus spinoletta*. Water Pipit. 23-24, 26-27 April 1973; 15, 29 April 1974; 1 May 1974.

°*Lanius ludovicianus*. Loggerhead Shrike. Two pairs nested in 1973 with one nest resulting in 4 fledglings. A single sighting on 29 April was the only 1974 record.

°*Vireo gilvus*. Warbling Vireo. 29 May 1974.

°°*Vermivora celata*. Orange-crowned Warbler. 5 May 1973.

Dendroica petechia. Yellow Warbler. Previously recorded on islands (Behle 1958). Common 8-13 May 1973, 6-24 May 1974.

°*Dendroica coronata auduboni*. Yellow-rumped Warbler. 25 April 1973; 4 May 1973; 30 April 1974; 1, 7, 11, 15, 22, 29 May 1974. *D.c. coronata*. 16 May 1973.

°°*Dendroica nigrescens*. Black-throated Gray Warbler. 9-10 May 1974.

°°*Geothlypis tolmiei*. MacGillivray's Warbler. 6, 8 May 1973; 2, 14, 22-24, 28 May 1974.

°°Wilsonia pusilla. Wilson's Warbler. 8 May 1973; 6, 10-11, 22-23, 28 May 1974.

°*Setophaga ruticilla*. American Redstart. 21 May 1974.

°*Sturnella neglecta*. Western Meadowlark. 12 May 1972, 25-26 April 1973, 5 May 1973, 1-2 May 1974.

Xanthocephalus xanthocephalus. Yellow-headed Blackbird. Previously recorded on Gunnison Island (Behle 1958). 28 May 1972; 23-24 April 1973; 5, 14, 23 May 1973; 22-23, 29 May 1974.

°*Agelaius phoeniceus*. Red-winged Blackbird. 15-16 April 1972; 24 April 1973; 3, 5-6 May 1973.

°*Icterus galbula*. Northern Oriole. 4 May 1973, 22 May 1974.

°*Euphagus cyanocephalus*. Brewer's Blackbird. 24, 26-27 April 1973; 3-8, 14, 23 May 1973; 15 April 1974; 3, 23 May 1974.

Molothrus ater. Brown-headed Cowbird. Previously recorded on Gunnison Island (Behle 1958). 24 April 1973; 22-24, 29 May 1974; 24-25 July 1974

Pheucticus melanocephalus. Black-headed Grosbeak. Previously recorded (Behle 1958), but not seen 1972-1974.

°*Passerina amoena*. Lazuli Bunting. 6 May 1973.

°*Carpodacus mexicanus*. House Finch. 16 April 1972, 10 May 1974.

°*Pipilo chlorura*. Green-tailed Towhee. 4-8, 14, 23 May 1973; 1-2, 7-10, 14-15, 22-23, 29 May 1974.

Pipilo erythrophthalmus. Rufous-sided towhee. 15-16 April 1972, 4 May 1973, 7 May 1974.

°*Passerculus sandwichensis*. Savannah Sparrow. 29-30 April 1974.

°*Pooecetes gramineus*. Vesper Sparrow. 4-6 May 1973, 30 April 1974, 9 May 1974.

°*Chondestes grammacus*. Lark Sparrow. 4-5, 7 May 1973; 7, 10, 14, 21-22 May 1974.

°*Aimophila bilineata*. Black-throated Sparrow. 2-3 May 1973.

°°*Aimophila belli*. Sage Sparrow. 16 April 1972.

°°*Junco hyemalis*. Dark-eyed Junco. 5-6, 23-24, 26-27 April 1973; 13 May 1973; 15 April 1974.

°°*Junco caniceps*. Gray-headed Junco. 8 May 1973, 8 May 1974.

°°*Spizella arborea*. Tree Sparrow. 21 May 1974.

Spizella passerina. Chipping Sparrow. Previously recorded on Gunnison Island (Behle 1958). 13 May 1973; 30 April 1974; 1, 6-7, 14-15, 22, 24, 29 May 1974.

°°*Spizella pallida*. Clay-colored Sparrow. 9 May 1974.

°*Spizella breweri*. Brewer's Sparrow. 5-6, 8 May 1973; 30 April 1974; 9-10, 15, 23-24 May 1974.

°*Zonotrichia leucophrys*. White-crowned Sparrow. 15-16 April 1972; 23 April 1973; 3, 5-6 May 1973; 29 April 1974; 2, 6-10, 14-15, 23-24 May 1974.

°°*Zonotrichia melodia*. Song Sparrow. 15 April 1972.

COMMENTS ON THE AVIFAUNA

The avifauna of Gunnison and Cub islands consisted primarily of transient species. Of 112 species, 104 (93 percent) occurred as transients. Transients which found abundant food on the islands (e.g., individuals of the Columbidae and Fringillidae) were present in larger numbers and for longer periods of time than those not finding food (e.g., individuals of the Anatidae and Scolopacidae). None of the species occurring as transients were present long enough to be considered seasonal residents. The Short-eared Owl was the only non-nesting species considered to be a resident.

Species observed on the two islands were typical of those occurring in similar habitats throughout northern Utah. Some notable exceptions were the "sedentary" Dipper and Mountain Chickadee, both being 40 km from their typical habitats. The Black-billed Magpie (*Pica pica*), which is abundant in the region, was not seen on the islands.

Few species of birds actually nested on Gunnison and Cub islands relative to the surrounding Great Basin desert. Many of the desert species (Mourning Dove, Horned Lark, Lark Sparrow, Brewer's Sparrow) were observed on the islands in large flocks during spring migration. The impoverished community of breeding birds may reflect poorer nesting habitat for these species. Habitats for Loggerhead Shrike appeared marginal (as developed by Johnson 1965:121), with two pairs breeding in 1973, where none bred in 1972 or 1974.

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VARYING PREVALENCE OF *TAENIA TAENIAEFORMIS* STROBILOCERCI IN *MICROTUS PENNSYLVANICUS* OF MONTANA

Richard H. McBee, Jr.[1]

Abstract.— Of 42 *Microtus pennsylvanicus* trapped 1 km from Bozeman, Montana, 14 (33.3 percent) were infected by strobilocerci of *Taenia taeniaeformis*, while only one (2.1 percent) of 47 was infected at a rural site 16 km from Bozeman. The higher incidence of the primary host, domestic cats, is believed to account for the higher rate of infection near Bozeman.

Microtus pennsylvanicus has previously been reported as an intermediate host for *Taenia* (=*Hydatigera*) *taeniaeformis* by Rausch and Tiner (1949, Am. Midl. Nat. 41:665–694), who found 43 of 570 voles in the north central U.S. infected, and by Kinsella (1967, Can. J. Zool. 45:269–274), who found strobilocerci in 2 of 25 voles from western Montana.

Survey data collected in southwestern Montana in 1971 indicated that the prevalence of infection of *M. pennsylvanicus* with *T. taeniaeformis* strobilocerci may vary widely according to the proximity of the voles to large numbers of primary hosts such as the domestic cat.

Voles were trapped from boggy areas on two different sites near the city of Bozeman, Gallatin County, Montana. The first area was located just outside the city limits and within easy range of numerous house cats. The second area was located approximately 16 km (10 mi) from Bozeman in farm land, with the nearest residence more than 1 km (.6 mi) away.

A total of 42 *M. pennsylvanicus* was trapped from the first area, and their livers were examined for the strobilocerci of *T. taeniaeformis*. Infected voles totaled 14 (33.3 percent positive), with several animals having multiple cysts (an average 1.86 cysts per infected animal). A total of 47 voles was examined from the second area and, of these, one animal (2.1 percent) was found to be infected, with its liver harboring a single cyst.

The low incidence of infection of the rural *M. pennsylvanicus* with *T. taeniaeformis* is attributed to the lack of large numbers of primary hosts in the area.

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AN ANNOTATED LIST OF THE AQUATIC INSECTS OF SOUTHEASTERN IDAHO, PART II: TRICHOPTERA

Robert L. Newell[1] and G. Wayne Minshall[2]

Abstract.— Distribution records for the Trichoptera occurring in the southeastern one-third of Idaho are summarized based on published records and collections by the authors and their colleagues. The study revealed representatives of 13 families, 37 genera, and 84 species. Several species were collected for the first time in Idaho, including: *Hesperophylax magnus*, *Limnephilus frijole* and *L. thorus*, *Psychoglypha ormiae*, *Ceraclea annulicornis* and *C. copha*, *Polycentropus crassicornis*, *Tinodes provo*, and *Agrypania dextra*.

The Trichoptera (caddisflies) comprise one of several purely aquatic orders of insects. This small order is composed of some 30 families and 5,000 species distributed throughout the world. This study revealed representatives of 13 families, 37 genera, and 84 species. Some genera were captured, but a species determination was not possible and these are not listed. The study area includes the southeastern one-third of Idaho (Fig. 1). Note that this figure corrects and replaces the one given in Newell and Minshall (1976).

Information on geographical distribution of caddisflies in Idaho is widely distributed. Local investigations that included distributional records are Andrews (1972), Givens (1976), Newell and Potter (1973), Nimmo (1971), Kroger (1970), Smith (1965, 1968a, 1968b, 1969), Terch (1972), Winger (1968) and Wold (1974). Other Idaho records are available in Denning (1948, 1950, 1954, 1956, 1958, 1965a, 1965b, 1970, 1973), Denning and Blickle (1972), Gordon (1974), Milne and Milne (1938), Hornung and Barr (1970), Ross (1941, 1944, 1947, 1951, 1952, 1956), and Schmid (1968, 1970). Identification of immature caddisflies will be aided greatly by the key of Wiggins (1977). Several of the above-listed papers include taxonomic keys to adult caddisflies. The taxonomic treatment used throughout this paper is that of Ross (1967).

Several species were collected for the first time in Idaho, and these include: *Hesperophylax magnus*, *Limnephilus frijole* and *L. thorus*, *Psychoglypha ormiae*, *Ceraclea annulicornis* and *C. copha*, *Polycentropus crassicornis*, and *Tinodes provo* and *Agrypania dextra*.

Individuals of the family Hydropsychidae were the most frequently encountered. Individuals of *Hydropsyche occidentalis* were extremely abundant in the main Snake River, often visible in swarms of thousands of adults. Several species were encountered only once, either because of their small populations or because their habitats were difficult to collect (i.e., high altitude streams).

The large number of species collected is probably indicative of the diversity of available habitats, ranging from spring seeps to large mountain rivers and from silty lowland streams and irrigation reservoirs to constant temperature springs.

The authors would like to thank the many people who contributed time, effort, and specimens for this study. They would also like to thank Dr. Norman H. Anderson and Dr. A. P. Nimmo for their suggestions concerning the manuscript and Dr. Donald G. Denning for his help in identifying specimens.

Family hydropsychidae

1. *Arctopsyche grandis* (Banks).—Bear Lake Co.: St. Charles Cr. Blaine Co.: Big

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Wood R. Bonneville Co.: Pine Cr., Rainey Cr., Snake R. (S. Fk.). Butte Co.: Little Lost R. Caribou Co.: Portneuf R., Tin Cup Cr. Clark Co.: Birch Cr., Medicine Lodge Cr. Custer Co.: Big Lost R.

2. *Cheumatopsyche campyla* Ross.—Bonneville Co.: Idaho Falls. Franklin Co.: Preston. Gooding Co.: Niagara Springs, Snake R. Twin Falls Co.: Rock Cr.

3. *Cheumatopsyche enonis* Ross.—Bonneville Co.: Idaho Falls. Twin Falls Co.: Salmon Falls Cr.

4. *Cheumatopsyche pettiti* (Banks).—Bear Lake Co.: Dingle. Bonneville Co.: Brockman Cr. Caribou Co.: Lane's Cr. Oneida Co.: Deep Cr.

5. *Hydropsyche bifida* Banks.—Bannock Co.: Mink Cr.

6. *Hydropsyche californica* Banks.—Bannock Co.: Portneuf R. Bingham Co.: Spring Cr. Gooding Co.: Niagara Springs. Oneida Co.: Deep Cr. Owyhee Co.: Snake R. Power Co.: Snake R.

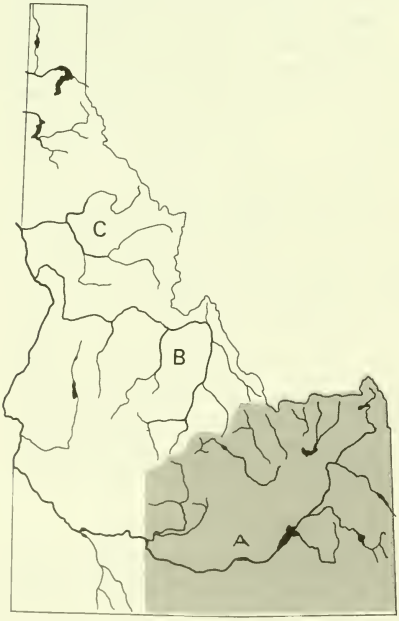

Fig. 1. An outline map of Idaho showing the location of the study area (shaded portion) in relation to the major river drainage systems. *Note:* This figure replaces the one given in Newell and Minshall (1976) in which the shaded area was lost in the printing process.

7. *Hydropsyche cockerelli* Banks.—Bonneville Co.: Snake R. Teton Co.: Teton R.

8. *Hydropsyche occidentalis* Banks.—Bannock Co.: Portneuf R. Caribou Co.: Portneuf R. Fremont Co.: Falls R. Gooding Co.: Niagara Springs. Oneida Co.: Deep Cr. Power Co.: Snake R.

9. *Hydropsyche oslari* Banks.—Bannock Co.: Mink Cr. Bonneville Co.: Pine Cr., Rainey Cr. Teton Co.: Trail Cr.

10. *Parapsyche almota* Ross.—Bannock Co.: Mink Cr.

11. *Parapsyche elsis* Milne.—Blaine Co.: Big Wood R. Bonneville Co.: Rainey Cr. Butte Co.: Little Lost R. Franklin Co.: Cub R. Lemhi Co.: Little Lost R.

FAMILY POLYCENTROPODIDAE

12. *Polycentropus cinereus* Hagen.—Bingham Co.: Spring Cr.

13. *Polycentropus crassicornis* Walker.—Bingham Co.: Spring Cr.

FAMILY PSYCHOMYIIDAE

14. *Psychomyia flavida* Hagen.—Fremont Co.: Falls R., Robinson Cr., Snake R. (Henry's Fk.). Power Co.: Snake R.

15. *Tinodes provo* Ross.—Gooding Co.: Niagara Springs. Oneida Co.: Deep Cr.

FAMILY PHILOPOTAMIDAE

16. *Dolophilodes aequalis* (Banks).—Bannock Co.: Mink Cr., Rapid Cr. Bonneville Co.: Rainey Cr.

17. *Wormaldia gabriella* (Banks).—Bannock Co.: Mink Cr.

FAMILY RHYACOPHILIDAE

18. *Rhyacophila acropedes* Banks.—Bannock Co.: Mink Cr. Bonneville Co.: Pine Cr., Rainey Cr. Butte Co.: Little Lost R. Clark Co.: Birch Cr., Medicine Lodge Cr. Gooding Co.: Niagara Springs. Teton Co.: Trail Cr.

19. *Rhyacophila alberta* Banks.—Bonneville Co.: Rainey Cr. Teton Co.: Trail Cr.

20. *Rhyacophila angelita* Banks.—Bonneville Co.: Rainey Cr.

21. *Rhyacophila bifila* Banks.—Fremont Co.: Falls Cr.

22. *Rhyacophila coloradensis* Banks.—Bonneville Co.: Pine Cr., Rainey Cr. Gooding Co.: Hagerman Springs, Niagara Springs. Teton Co.: Trail Cr.

23. *Rhyacophila hyalinata* Banks.—Butte Co.: Little Lost R.

24. *Rhyacophila narvae* Navas.—Butte Co.: Little Lost R.

25. *Rhyacophila pellisa* Ross.—Bannock Co.: Mink Cr. Bonneville Co.: Rainey Cr. Lemhi Co.: Little Lost R.

26. *Rhyacophila vaccua* Milne.—Clark Co.: Birch Cr. Lemhi Co.: Little Lost R. Teton Co.: Trail Cr.

27. *Rhyacophila vagrita* Milne.—Bonneville Co.: Rainey Cr.

28. *Rhyacophila vao* Milne.—Bannock Co.: Mink Cr. Blaine Co.: Big Wood R.

29. *Rhyacophila verrula* Milne.—Bonneville Co.: Rainey Cr. Lemhi Co.: Little Lost R. Teton Co.: Trail Cr.

30. *Rhyacophila vocala* Milne.—Bonneville Co.: Rainey Cr.

FAMILY GLOSSOSOMATIDAE

31. *Agapetus montanus* Denning.—Clark Co.: Beaver Cr.

32. *Anagapetus debilis* Ross.—Custer Co.: Wildhorse Cr.

33. *Glossosoma alascensis* Banks.—Bonneville Co.: Pine Cr. Custer Co.: Wildhorse Cr. Fremont Co.: Robinson Cr. Teton Co.: Trail Cr.

34. *Glossosoma idaho* Ross.—Fremont Co.: Falls R. Gooding Co.: Niagara Springs.

35. *Glossosoma intermedium* (Klapalek).—Teton Co.: N. Fk. Teton R.

36. *Glossosoma montana* Ross.—Bonneville Co.: Snake R. (S. Fk.). Fremont Co.: Falls R.

37. *Glossosoma schuhi* Ross.—Bannock Co.: Mink Cr.

38. *Glossosoma traviatum* Banks.—Fremont Co.: Falls R.

39. *Glossosoma velona* Ross.—Bannock Co.: Mink Cr. Bingham Co.: Spring Cr. Caribou Co.: Portneuf R. Teton Co.: Teton R.

40. *Glossosoma verdona* Ross.—Bonneville Co.: Rainey Cr.

41. *Protoptila coloma* Ross.—Fremont Co.: Warm R.

FAMILY HYDROPTILIDAE

42. *Ochrotrichia logana* (Ross).—Gooding Co.: Niagara Springs.

43. *Ochrotrichia stylata* (Ross).—Power Co.: Snake R.

FAMILY LEPIDOSTOMATIDAE

44. *Lepidostoma pluvialis* (Milne).—Bannock Co.: Mink Cr.

45. *Lepidostoma podager* McLachlan.—Bannock Co.: Mink Cr.

46. *Lepidostoma strophis* Ross.—Bingham Co.: Spring Cr. Gooding Co.: Niagara Springs. Oneida Co.: Daniels Spring.

47. *Lepidostoma unicolor* (Banks).—Bannock Co.: Mink Cr. Bonneville Co.: Pine Cr.

FAMILY LIMNEPHILIDAE

48. *Amphicosmoecus canax* (Ross).—Bingham Co.: Spring Cr. Bonneville Co.: Rainey Cr. Custer Co.: Little Lost R. Fremont Co.: Snake R. (Henry's Fk.). Teton Co.: Trail Cr.

49. *Apatania chasica* (Denning).—Blaine Co.: Big Wood R. Bonneville Co.: Rainey Cr.

50. *Apatania comosa* Denning.—Bonneville Co.: Pine Cr.

51. *Chyranda centralis* (Banks).—Bannock Co.: Mink Cr. Custer Co.: Wildhorse Cr.

52. *Ecclisomyia maculosa* Banks.—Lemhi Co.: Little Lost R. Teton Co.: Trail Cr.

53. *Ecclisomyia simulata* Banks.—Bonneville Co.: Rainey Cr.

54. *Hesperophylax consimilis* (Banks).—Bannock Co.: Mink Cr. Bonneville Co.: Rainey Cr. Caribou Co.: Portneuf R.

55. *Hesperophylax incisus* Banks.—Bannock Co.: Mink Cr. Bonneville Co.: Rainey Cr. Fremont Co.: Buffalo R.

56. *Hesperophylax magnus* Banks.—Bonneville Co.: Rainey Cr.

57. *Lenarchus brevipennis* (Banks).—Fremont Co.: Pond near Upper Mesa Falls.

58. *Limnephilus challisa* Denning.—Blaine Co.: Hyndman Cr.

59. *Limnephilus extractus* Walker.—Fremont Co.: Snake R. (Henry's Fk.).

60. *Limnephilus frijole* Ross.—Oneida Co.: Deep Cr.

61. *Limnephilus spinatus* Banks.—Bannock Co.: Hawkins Res. Bonneville Co.: Pond near Palisades Res. Caribou Co.: Grey's Lake. Fremont Co.: Snake R. (Henry's Fk.). Oneida Co.: Daniels Res.

62. *Limnephilus thorus* Ross.—Bingham Co.: Clear Cr.

63. *Neophylax occidentis* Banks.—Lemhi Co.: Firebox Cr.

64. *Neophylax splendens* Denning.—Bannock Co.: Mink Cr. Bonneville Co.: Rainey Cr.

65. *Neothremma alicia* Banks.—Teton Co.: Trail Cr.

66. *Oligophlebodes minutus* (Banks).—Bannock Co.: Gibson Jack Cr., Mink Cr.

67. *Oligophlebodes ruthae* Ross.—Camas Co.: Big Lost R.

68. *Oligophlebodes sierra* Ross.—Bear Lake Co.: Bloomington Cr., St. Charles Cr. Bonneville Co.: Rainey Cr.

69. *Onocosmoecus atripes* (Hagen).—Bannock Co.: Mink Cr. Bingham Co.: Spring Cr. Bonneville Co.: Rainey Cr.

70. *Onocosmoecus unicolor* (Banks).—Bannock Co.: Mink Cr. Bingham Co.: Spring Cr. Bonneville Co.: Rainey Cr. Teton Co.: Trail Cr.

71. *Psychoglypha ormiae* (Ross).—Bonneville Co.: Rainey Cr.

72. *Psychoglypha subborealis* (Banks).—Bannock Co.: Mink Cr. Bonneville Co.: Rainey Cr.

FAMILY PHRYGANEIDAE

73. *Agrypania dextra* Ross.—Bannock Co.: Pond in Indian Rocks St. Park.

FAMILY BRACHYCENTRIDAE

74. *Amiocentrus aspilus* (Ross).—Bingham Co.: Clear Cr., Spring Cr. Bonneville Co.: Rainey Cr. Teton Co.: Teton R.

75. *Brachycentrus americanus* (Banks).—Bannock Co.: Mink Cr. Bingham Co.: Clear Cr. Bonneville Co.: Pine Cr. Caribou Co.: Portneuf R.

76. *Brachycentrus occidentalis* Banks.—Bingham Co.: Spring Cr. Bonneville Co.: Rainey Cr. Butte Co.: Little Lost R. Clark Co.: Beaver Cr., Birch Cr., Camas Cr., Medicine Lodge Cr.

FAMILY HELICOPSYCHIDAE

77. *Helicopsyche borealis* (Hagen).—Bingham Co.: Clear Cr. Caribou Co.: Blackfoot R., Lane's Cr., Portneuf R. Clark Co.: Birch Cr., Camas Cr. Teton Co.: Warm Spring Cr.

FAMILY LEPTOCERIDAE

78. *Ceraclea annulicornis* (Stephens).—Power Co.: Snake R.

79. *Ceraclea copha* (Ross).—Power Co.: Snake R.

80. *Ceraclea tarsipunctata* (Vorhies).—Bingham Co.: Snake R.

81. *Ceraclea transversa* (Hagen).—Cassia Co.: Small stream near Malta.

82. *Mystacides alafimbriata* Griffin.—Teton Co.: Pond near Teton R.

83. *Nectopsyche diarina* (Ross).—Blaine Co.: Big Wood R. Oneida Co.: Deep Cr.

84. *Triaenodes frontalis* Banks.—Bingham Co.: Spring Cr. Oneida Co.: Deep Cr.

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A NEW STATUS FOR *PENSTEMON CYANANTHUS* HOOK. SSP. *SUBGLABER* PENNELL (SCROPHULARIACEAE)

Stephen L. Clark[1]

Abstract.— *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell, a plant found frequently in northwestern Utah, southeastern Idaho, and southeastern Wyoming, is elevated to species status. A new name, *Penstemon holmgrenii* Clark is proposed because *P. subglaber* is preoccupied.

Penstemon cyananthus Hook. ssp. *subglaber* Pennell is a tall, densely puberulent to pubescent, blue-flowered plant found commonly within sage and pinyon-juniper areas of northwestern Utah, southeastern Idaho, and southwestern Wyoming. Pennell described it in 1920 and separated it from *P. cyananthus* ssp. *cyananthus* on the basis that the leaves of the subspecies are more lanceolate and more densely puberulent. Investigations by this writer suggest, however, that other differences exist. *Penstemon cyananthus* ssp. *cyananthus* is never pubescent. The staminode of *P. cyananthus* ssp. *subglaber* is densely covered with long yellow hairs, and the two taxa are not sympatric. These differences suggest to the writer that the subspecies should be elevated to species status.

The following new name is proposed to replace the epithet *Penstemon cyananthus* Hook. ssp. *subglaber* Pennell: *Penstemon holmgrenii* Clark nom. nov., based on *P. cyananthus* Hook. ssp. *subglaber* Pennell in Scrophulariaceae of the Rocky Mountain States. Contributions from the United States National Herbarium 20(9):313–381. Not *P. subglaber* Rydb. Named in honor of Arthur H. Holmgren, a friend who first guided me into studies in *Penstemon*.

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RANGE EXTENSION OF *TRIONYX SPINIFERUS EMORYI* INTO UTAH (REPTILIA)

Carlos Y. Roby[1] and Earl C. Loveless[1]

Abstract.— Four Texas Spiny Softshell Turtles (*Trionyx spiniferus emoryi*) were collected near St. George, Utah. This represents a range extension of 65 km northward into Utah from Nevada.

Of the six subspecies of *Trionyx spinifer* in the United States, only the Texas Spiny Softshell Turtle, *Trionyx spiniferus emoryi* (Agassiz), is known to occur in the Colorado River drainage. Miller (Copeia 1946:46) suggested that the species was introduced into this area around the turn of the century when a dam of an artificially stocked pond on a ranch in Grant County, New Mexico, gave way. This permitted the softshell access to the Gila River, a tributary of the Colorado River.

On 24 July 1976, four *T. s. emoryi* were collected in a small pond within 50 m of the Virgin River, approximately 6 km (4 mi) north of St. George, Utah. The specimens include three females and one male (deposited at Brigham Young University, BYU 41646-9), with plastral lengths of 12.20, 11.0, 9.5, and 9.1 cm. Seven others were sighted in this pond and thirteen others in the Virgin River.

This represents a northern extension of the known range (Webb, 1962, Univ. Kansas Publ. Mus. Nat. Hist. 13(10):429–611) of approximately 65 km (40 mi) from the previous record 2 km (1.5 mi) above Mesquite, Clarke County, Nevada, and a total extension of approximately 720 km (450 mi) since its introduction into the Gila River. We wish to thank Dr. Andrew H. Barnum for his assistance and the Associated Students of Brigham Young University for funding this project. We also thank Dr. Wilmer W. Tanner for his suggestions.

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THE LIFE CYCLE OF *HYDROPERLA CROSBYI* (PLECOPTERA: PERLODIDAE)[1]

Reed Y. Oberndorfer[2] and Kenneth W. Stewart[2]

Abstract.— *Hydroperla crosbyi* in Texas exhibited a univoltine, fast life cycle over the three-year study period. Adults emerged in February-March when mean daily stream temperature reached ca. 15 C. Reared females in the lab deposited up to three egg masses. Mean fecundity of dissected females was 787 eggs/female. Oviposition in the field was observed and described.

Eggs were triangular in cross section, brown, and measured 400 μm X 535 μm. They underwent an ca. seven-month diapause until mean daily stream temperature decreased to 18 C. Eyespots appeared, and hatching followed in two to three weeks. First instar nymphs were measured and described. Male and female nymphs underwent 12 and 14 instars, respectively, and could be sexed by the sixth. Fast growth occurred in the coldest season and Simuliidae and Chironomidae larvae were preferred food throughout development.

Eggs contained a mean of 6.21 cal/mg. Ash-free mean caloric value of last instar nymphs was 6.0 cal/mg. Adult males and females lost 33.8 percent and 57.6 percent, respectively, of their caloric pool through their ca. 12 days of life.

The life cycles and ecology of North American Plecoptera are relatively unknown. The classic works of Needham and Claassen (1925), Claassen (1931), Frison (1929, 1935, 1942), and Ricker (1952) were primarily taxonomic, with a few largely descriptive notes on morphology, life cycle events, and ecology. Detailed early studies were made by Wu (1923) for *Soyedina vallicularia* (Wu) and Holdsworth (1941a, b) for *Allonarcys proteus* (Newman). Recent papers by Minshall and Minshall (1966), Harper and Pilon (1970), Schwarz (1970), Tarter and Krumholz (1971), Radford and Hartland-Rowe (1971a, b), Harper and Hynes (1970, 1972), Harper (1973a, b), Vaught and Stewart (1974), Stanford (1975), Cather and Gaufin (1975), Hynes and Hynes (1975), and Hynes (1976) are indicative of a resurgent interest in Plecoptera life cycles as supportive knowledge for structural and functional studies at the population and community level.

The only detailed autecological study of a southwestern Nearctic stonefly was reported by Vaught and Stewart (1974) for *Neoperla clymene* (Newman), a widespread species occurring only in large, permanent rivers. Life cycles of southwestern species should differ markedly from those of boreal species (Harper and Hynes 1972, Harper 1973a, b), due to post-Pleistocene adaptation to drier, warmer climates, and the effects of stream permanence and physicochemical conditions.

Hydroperla crosbyi (Needham and Claassen) is a large perlodid stonefly that is widely distributed throughout the Mississippi Valley from Indiana and Illinois to Arkansas and Oklahoma (Ricker 1952). Stewart et al. (1974) first reported the species from Texas. It is common in streams across the Blackland Prairie into the Edwards Plateau and Eastern and Western Cross Timbers in Texas, and it appears to be a dominant species in the macrobenthic community of Clear Creek in Denton County, Texas, where this study was made. Presence of small nymphs in December, and larger nymphs and adults in March and April, had indicated a fast cycle (Hynes 1970). No previous life cycle studies have been published for any *Hydroperla* species. Stewart and Stark (1977) described the reproductive mor-

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phology and mating behavior of *H. crosbyi*, and Frison (1935) reported nymphal microdistribution and food habits. The purpose of this research was to make a thorough autecological investigation of *H. crosbyi*, with emphasis on its life cycle.

STUDY STREAM

All sampling and observations were done at several sites along Clear Creek in Denton County, Texas, from Highway 455, ca. 0.5 km west of Bolivar, Texas, to the bridge on Highway 428, ca. 4 km northeast of Denton. Clear Creek originates in Montague County, Texas, and flows through Cooke and Denton counties, merging with Elm Fork of the Trinity River ca. 5 km above Lake Lewisville. Stream discharge is highly variable, depending upon season and rainfall, with the highest levels usually occurring in spring and lowest levels occurring during the summer. In dry years, the stream becomes intermittent during July-September. The substrate consists mainly of sand, with gravel and rock rubble riffles. Packs of leaves and other debris collect on large rocks and fallen tree limbs in riffle areas. The streamside forest is dominated by cottonwood (*Populus deltoides*), sycamore (*Platanus occidentalis*), black willow (*Salix nigra*), and several species of elm (*Ulmus* spp.). As leaves become conditioned by microbes, a successive invasion by macrobenthos, including shredders, collectors, scrapers, and predators, ensues (Cummins 1974). The role of *H. crosbyi* in this sequence was suspected to be that of a dominant macropredator.

MATERIALS AND METHODS

Seasonal growth, instar analysis, food habits, sex ratios, and numbers/m^2 were determined from quantitative and qualitative samples taken from January 1974 through March 1976. Biweekly qualitative samples were taken from October through March in each year except in October and November 1974, when heavy fall rains prevented access to the stream. A fine (363 μm) mesh net was used when earlier life stages were present, and a larger (1 mm) mesh kick net was used for later instars. Specimens were either preserved in 70 percent isopropyl alcohol or transported live to the laboratory for rearing studies. Six quantitative samples were taken each month from November 1975 to March 1976 by kicking up an area of 25 cm^2 in front of a fine (363 μm) mesh net; care was taken to sample all typically available habitat types, including leaf debris and rocky substrate. These were preserved in 70 percent isopropyl alcohol and taken to the laboratory for sorting and identification of all organisms. Last instar exuviae were collected in March 1976, to aid in a more precise estimate of the adult sex ratio since adults were difficult to obtain in the field. In an attempt to find eggs or smaller instars, 5 liters of damp substrate from areas with no surface flow and from pools were collected monthly during the period of March through September 1974, preserved in 99 percent isopropyl alcohol, and brought to the laboratory for elutriation (Stewart 1975).

Aspects of adult emergence, mating, and oviposition were determined from field and laboratory observations. The longevity of laboratory-reared adults was determined by holding them in 8-dram, cotton-stoppered, glass shell vials at room temperature, ca. 24 C.

Caloric values of last instar male and female nymphs and their exuviae, newly emerged virgin males, spent (postmated) males, newly emerged virgin females with ova and after ova removal by dissection, spent females (after oviposition), and deposited egg masses were determined and compared. Energy allocated to reproduction (Pr) was equated to the caloric contents of the total amount of eggs deposited by a female. An instantaneous measure of reproductive effort (IRE) was expressed as a percentage of energy going to production of eggs (Pr) and to growth (Pg). After obtaining live weights, individuals were dried in a vacuum oven at 80 C (–15 psi) for 24 hours, weighed, ground with a mortar and pestle, and pressed into pellets of known weights (10-20 mg). The pellets were combusted in a Gentry-Weigert modification of a Phillipson microbomb calorimeter (Phillipson 1964). The dry weight of material not combusted was considered to be ash weight; therefore, caloric data were expressed as calories/mg ash-free dry weight. Organisms were not bombed individually, but pooled to produce the pellets.

Groups of eggs deposited in March by reared, mated females were incubated in 1974 and 1976. They were held in loosely covered 8-dram vials at 22 ± 2 C until October (1974) and September (1976), then transferred into a Percival E-50 environmental chamber, lowered 1 C per day down to 18 C.

Eggs "in uteri" and deposited eggs were counted, photographed, measured, and described, with special attention given to any gelatinous layers and/or other attachment structures and chorionic sculpturing (Stewart et al. 1969). Scanning electron micrographs were made using an ISI Mini-SEM.

First instar nymphs, hatched from eggs obtained in March 1974, were preserved in 70 percent isopropyl alcohol for drawings and descriptions. The interocular distance of these and field-collected nymphs was measured using a calibrated ocular micrometer, and sex was determined when possible. Live nymphs were placed in styrofoam cups with creek water and kept in the environmental chamber at simulated creek temperature and photoperiod to determine size changes and to rear them to adults. After one sampling date in February 1976, 40 last instar nymphs were divided into three groups and kept at three constant temperatures, 7 C, 15 C, and 25 C, respectively, to determine the effect of temperature on the time required for development and emergence.

Size-frequency histograms, constructed from interocular distances of field-collected nymphs, and the methods of Cassie (1954) and Janetschek (1967) were used to interpret growth and instar development. To supplement these analyses and aid in interpretation, field-collected nymphs of different sizes were reared to successive instars.

Food habits were determined by foregut analysis (Richardson and Gaufin 1971). Forage ratio (FR) (Hess and Swartz 1941) and electivity (E) (Ivlev 1961) were calculated for determination of food preferences.

Stream temperature was taken on each sampling date with a total immersion thermometer. A seven-day continuous recording thermograph (Tempscribe remote bulb recorder) was placed in the stream in June 1975 and left for the remainder of the study. Stream flow was taken on each sampling date from August 1975 to March 1976, using a Kahl Pygmy Flow Meter calibrated at 0.4714 meters per revolution. Seasonal water samples were taken and analyzed for pH, conductivity, and alkalinity according to standard methods (American Public Health Association 1971).

RESULTS AND DISCUSSION

During the study, pH varied from 7.6 (summer 1975) to 8.1 (winter 1976), conductivity 530 μmhos (fall 1975) to 1,180 μmhos (summer 1975), and total alkalinity 212 ppm (fall 1975) to 408 ppm (winter 1976). Stream flow was highly variable, with the highest level observed in October-November 1974 and no flow in June-August 1974. From August 1975 to March 1976, stream flow remained relatively constant at ca. 1.4 m/sec. Temperature ranged from 30 C in June 1974 to 2 C in February 1976. Such highly variable and intermittent conditions of Clear Creek are typical of moderate-sized streams on the western edge of the temperate deciduous forest. Life cycle adjustments of stoneflies such as *H. crosbyi* and *Perlesta placida* (Hagen) through natural selection, which have enabled success in such harsh environments, were of prime interest in this study.

Other dominant insects associated with *H. crosbyi* in Clear Creek included *Isonychia sicca manca* (Eaton), *Choroterpes (Neochoroterpes) mexicanus* (Allen), *P. placida*, *Corydalus cornutus* (Linnaeus), *Hydropsyche simulans* (Ross), *Cheumatopsyche campyla* (Ross) and *C. lasia* (Ross).

ADULT.—*H. crosbyi* displayed a relatively spontaneous emergence, with adults occurring from mid-February through March during the three-year study period. A similar recurrent emergence pattern has been reported for several stonefly species (Nebeker 1971b, Müller 1973, Kerst and Anderson 1974). Average daily stream temperatures at the onset of emergence were ca. 15 C with 19 C maxima and 13 C minima. Emergence was essentially over and nymphs gone when average daily stream temperatures reached 22 C. As emergence progressed, there was a corresponding decline in nymphal populations. These observations and results of laboratory holding of mature nymphs in environmental chambers suggest that the mean daily stream temperature cue for emergence in *H. crosbyi* is ca. 15 C. Field-collected, mature nymphs held at 7, 19, and 25 C showed a highly significant difference ($P<0.01$) in the mean number of days to emergence, with most time ($\bar{X} = 44.8$ days) at 7 C, shortest successful emergence ($\bar{X} = 25.6$ days) at 19 C, and 100 percent mortality at 25 C.

The emergence of some stonefly species is apparently dependent on the number of degree days or temperature accumulation during nymphal development (Cummins 1974, Stanford 1975). Several investigators have indicated that events such as emergence and hatching result when a certain temperature cue is attained during periods of increasing or decreasing temperatures (Sheldon and Jewett 1967, Heiman and Knight 1970, Harper and Pilon 1970, Nebeker 1971a, b, Radford and Hartland-Rowe 1971, Sheldon 1972, Harper 1973a, b). The emergence response range (tolerance) to such cues is narrow in nymphs such as *H. crosbyi* and others, effectively synchronizing emergence into a short time period (Macan 1958, Nebeker and Gaufin 1967, Nebeker 1971c, Hynes and Hynes 1975). Since accurate temperature data were not available over successive seasons, and a major egg-incubation experiment was lost due to environmental chamber malfunction, it could not be determined whether temperature accumulation (Baskerville and Emin 1969) influenced the development and emergence of *H. crosbyi*.

Collections of cast exuviae indicated that mature nymphs crawled out of the water onto rocks or debris above the surface of the water or along the bank for transformation. Similar emergence has been reported for *Paragnetina media* (Walker) (Tarter and Krumholz 1971) and *Isoperla transmarina* (Newman) (Harper 1973a). Adults then either fly or walk to streamside vegetation or debris near the water. Preemergent nymphal sex ratios were ca. 1:1, but collections of exuviae in the middle of the emergence period in March 1976 favored females, 1.0 ♂ :1.5 ♀ , indicating at least a slightly protandrous emergence. Schwarz (1970), Heiman and Knight (1970), Sheldon (1972), and Harper (1973a, b) have reported similar findings for other species.

A seasonal size variation was exhibited in adult *H. crosbyi*. The interocular distance decreased as emergence continued from a mean of 2.0 mm to 1.6 mm for females, and from 1.7 mm to 1.4 mm for males. Khoo (1968a), Schwarz (1970), Sheldon (1972), and Cather and Gaufin (1975) have shown similar variation, indicating that the emergence cue hurries smaller specimens so that full size is not attained (Khoo 1968a).

Adults did not feed, but they were observed to drink water; Hynes (1976) suggested this is probably true of all adult Systellognatha. Dissection indicated that the digestive tract was much reduced.

A period of two to five days is required for maturation of eggs in adult females. *Isoperla clio* (Newman) (Harper 1973a), *Isoperla goertzi* Illies, and *Diura bicaudata* (Linnaeus) (Schwarz 1970) require a similar egg maturation period. Males find females by a tactile or possibly by a pheromone response, and mating takes place on streamside vegetation or debris. Reproductive morphology, mating, and sperm transfer have been described by Stewart and Stark (1977). Sperm transfer in this species is external, and the aedeagus does not function as an intromittent organ. The species exhibits polygamous mating habits. Mated females flew to tree branches from 5 to 10 m above the stream on ca. the fifth day after emergence. An egg mass was extruded from the genital opening located at the rear of the abdominal sternum 8. Between ca. one to one-half hour before sunset, the female began her oviposition flight, approaching the site from upstream. She glided down and rested briefly on smooth water from 2 to 10 m from the head of a riffle. Contact with water and a slight movement of the abdomen resulted in separation of the mass, which then sank. The female was carried by the current ca. 1 m during this process, then rose off the water, flying back into adjacent trees. Laboratory-held females extruded up to two more egg masses over the next three to five days. Mean life span of mated adult males and females held in the laboratory at simulated light and temperature conditions was 11.4 and 11.6 days, respectively.

Mean numbers of eggs in successive masses for reared females were 330, 235, and 172, respectively. Fecundity of dissected, gravid females was from 442 to 1,418 eggs/♀, with a mean of 787/♀. Smaller females generally contained fewer eggs.

Deposited eggs had the highest caloric value (6.21 cal/mg) of any stage in the life cycle (Table 1). Mean caloric value of ca. 6.0 cal/mg ash-free for late instar *H. crosbyi* nymphs generally agree with those of Cummins and Wuycheck (1971) for immatures of various aquatic insects, McDiffett (1970) for *Pteronarcys scotti*, Lawton (1970, 1971) for *Pyrrhosoma nymphula* and its prey, Hofsvang (1973) for *Tipula excisa*, and Brown (1974) for *Corydalus cornutus*. Mean ash-free cal/mg of males were significantly different from females in all stages (Student's t; $P<0.05$). Few calories (16.34) appear to be lost in transformation, through loss of the exuvium (mostly epicuticle). Males lose 33.8 percent (27.13) of their caloric pool as metabolic heat through their ca. 12 days of life (Table 1).

A mean of 58.99 calories (deposited egg masses) constituted the energy allocated to reproduction (Pr) by females. However, a difference of 110.45 calories between newly emerged virgin females with ova and newly emerged virgin females with ova removed by dissection indicated that 51.46 calories might be resorbed by the female from undeposited eggs to be used for maintenance and metabolic costs involved in mating and oviposition. Energy allocated to growth (Pg) was estimated as the mean biocontent of a newly emerged virgin female with ova removed (106.95 calories), since the first instar was very small and its calories negligible. An instantaneous reproductive effort (IRE) was thus calculated as: Pr (58.99)/[Pr (58.99) + Pg (106.95)] = 35.5 percent. Another measure of IRE is the ratio of Pr to female carcass calories. Expressed this way, IRE of *H. crosbyi* was: Pr (58.99)/female carcass calories (106.95) = 55.1 percent. These values compare favorably with RE's determined by Brown (1974) for *C. corn-*

TABLE 1. Caloric values of major stages in the life cycle of *H. Crosbyi*.

Material	X̄ dry wt. (mg)	X̄ cal/mg Ash-free	N*	X̄ Biocontent (cal)
Male, last instar	19.4	6.01	10	116.59
Female, last instar	36.0	5.95	10	214.20
Last instar exuviae	3.0	5.43	10	16.34
Male, newly emerged (virgin)	14.2	5.66	10	80.37
Female, newly emerged (virgin with ova)	36.6	5.94	11	217.40
Female, newly emerged (virgin—ova removed)	18.6	5.75	7	106.95
Male, spent (postmated)	10.2	5.22	8	53.24
Female, spent (after oviposition)	18.7	4.93	8	92.19
Egg masses (total deposited/female)	9.5	6.21	2	58.99

*N = number of determinations

utus. A later discussion of food habits of *H. crosbyi* will show that its general food resources are similar to those of *C. cornutus*. Females lose 57.6 percent (125.21) of their caloric pool as metabolic heat and Pr during their adult life.

EGG.—Eggs are oval shaped, triangular in cross section, brown in color, and an average 400 μm wide by 535 μm long (Fig. 1). They are similar to descriptions of other perlodid eggs such as *Hydroperla fugitans* (Frison 1935), *Isogenoides frontalis* and *Isogenoides zionensis* (Knight et al. 1965), *Perlodes microcephala* and *Diura bicaudata* (Schwarz 1970), and *Pictetiella expansa* and *Isogenoides zionensis* (Baumann 1973). The chorion surface generally lacks the sculpturing so evident in perlids (Stark and Gaufin 1976a, b), the Isoperlinae, and other stoneflies. The crown ridge is reduced and from two to four micropyles occur near the middle on each of the three sides of the egg.

Each egg was enclosed by a gelatinous envelope, whose possible functions include: (1) prevention of desiccation after extrusion and prior to deposition, (2) action as a cementing substance to retain eggs in masses, and (3) attachment of individual eggs to substrate near the site of oviposition (Brinck 1949, Hynes 1970). A gelatinous mushroom-shaped attachment structure, emerging from the crown area of the egg, was prominent for at least the first 48 hours after deposition. Its "carapace" portion appeared as a shriveled mass in older eggs in water and those preserved in alcohol (Fig. 1). Both the envelope and the attachment mushroom were very effective in gluing eggs to glass or other substrate.

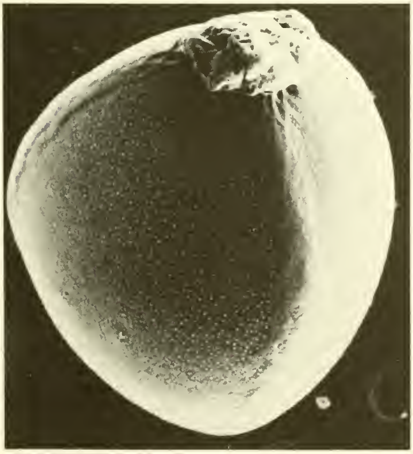

Fig. 1. *Hydroperla crosbyi* egg; SEM, 400x.

Eggs of *H. crosbyi* underwent a long, ca. seven-month diapause from February-March, when deposited, to October-November, when fall rains occurred and mean daily water temperature declined to ca. 18 C. Elutriation (Stewart 1975) of sand substrate from an area where there was no surface flow in July 1974 yielded one *H. crosbyi* egg and several *Perlesta placida* eggs that appeared turgid and alive. The diapause and development of eggs were similar to those of *Diura bicaudata* and *Brachyptera risi* (Khoo 1968b, c) and *Amphinemura delosa*, *A. linda*, *A. nigritta*, and *Prostoia completa* (Harper 1973b), in that eyespots appeared only two to three weeks before hatching.

One group of March 1974 eggs held at 25 ± 2 C until September, when the temperature was reduced 1 C every three to five days, hatched spontaneously at 19 C. This and early November appearance of first instar nymphs in Clear Creek suggest that rejuvenation of streams by fall rains and declining temperatures cue the termination of diapause. Another group of 2,000 March 1976 eggs, held in the laboratory at a constant 23 ± 1 C, hatched over an extended time period of five to eight months.

The diapause is a great advantage since it allows survival through hot summer, when water temperatures might be lethal to young nymphs and many of the intermittent streams inhabited by this species become dry. Several species such as *Zealeuctra arnoldi*, *Z. claasseni*, and *Z. hitei* and *Perlesta placida* that are endemic to, or extend their ranges into, the ecotone between the temperate deciduous forest and grassland are apparently capable of similar fast cycles. This adaptation is similar to several species reported by Hynes and Hynes (1976) in semiarid regions of Australia. Further work on their life cycles should provide some interesting comparisons with fauna of similar regions of the two continents. Many stoneflies undergo an egg or nymphal diapause to avoid adverse effects of extended cold or hot temperatures (Hartland-Rowe 1964, Khoo 1968a, b, c, Harper and Hynes 1970, 1972, Harper 1973a).

Eclosion (Fig. 2) follows the same general pattern reported by Heiman and Knight (1970) and Vaught and Stewart (1974); the chorion is torn, and the nymph pushes the hinged cap away and crawls out. Hatching in the field is apparently synchronous, since first instar nymphs in November 1975 were found only over a four-week period. Macan (1958) postulated that synchronous hatching is a disadvantage since competition for food and space would be very intense. This would only apply, however, in situations where numbers approach or exceed the carrying capacity. This theoretical asymptote (K) has not been defined for stream systems, where it would be expected to vary geographically and from year to year. Also, drift might play a large role in dispersing synchronously hatched nymphs.

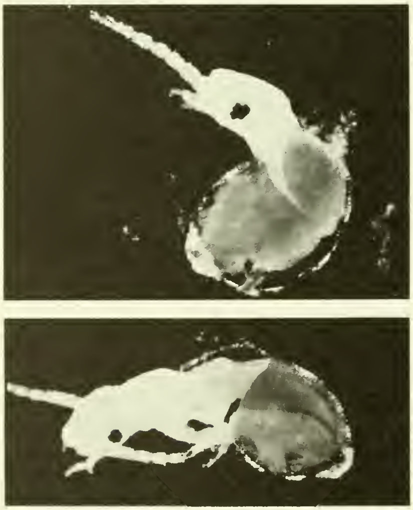

Fig. 2. Eclosion sequence; *Hydroperla crosbyi*.

Although both *H. crosbyi* and *Perlesta placida* occupy similar habitats, have similar diets, undergo an over-summer diapause, and have a relatively synchronous egg hatch (October-November), differential growth rates appear to separate them temporally. Nymphs of *H. crosbyi* grow faster through winter, leading to an emergence in February-March at the time when early instars of *P. placida* are just beginning their growth spurt, leading to an April-May emergence. A thorough comparison can be made in southwestern streams such as Clear Creek, when another current study of the life cycle of *P. placida* is completed (Rosalyn Snellen, personal correspondence).

Nymphs.—After hatching in October, nymphs grow rapidly through the winter until just prior to February-March emer-

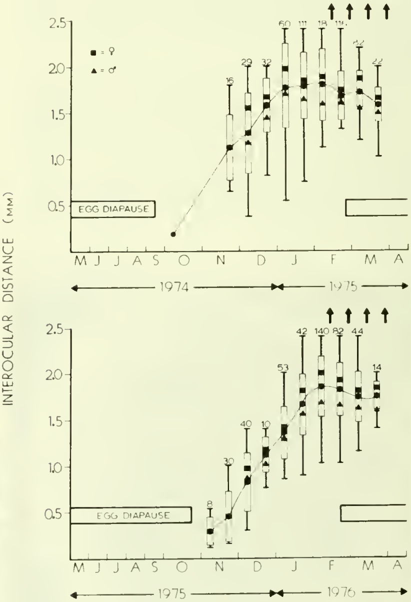

Fig. 3. Seasonal cycle and growth of *Hydroperla crosbyi*, March 1974 to March 1976, Clear Creek, Denton County, Texas: Vertical line = range, number at top of line = number measured, solid circle = mean, solid square and triangle within bars = mean female and male interocular distance, respectively, vertical bar = + & – 1SD, arrow = emergence.

gence (Fig. 3), when water temperatures are coldest (Fig. 4). The species thus fits Hyne's (1961) classification as an F_1 (fast) univoltine cycle. Similar cycles have been reported for *Isoperla clio* and *Isogenus decisus* (Minshall and Minshall 1966); *Amphinemura delosa, Prostoia completa*, and *Shipsa rotunda* (Harper 1973b); and *Capnia confusa, Utacapnia trava, U. columbiana, Doddsia occidentalis*, and *Taenionema pacifica* (Stanford 1975). This emphasizes the wide range of adaptation in Plecoptera nymphal growth characteristics since many species such as *Zapada columbiana*, (Hartland-Rowe 1964), *Taeniopteryx neubulosa, Nemura meyeri, A. borealis, N. cinerea, Leuctra hippopus, Capnia atra, Diura nanseni, Isoperla difformis, I. grammatica* (Svensson 1966), *Isoperla goertzi, Diura bicaudata* (Schwarz 1970), *Paragnetina media* (Heiman and Knight 1970), *Pteronarcys dorsata, Isoperla frontalis* (Nebeker 1971b), *Brachyptera risi, Protonemoura meyeri, Amphinemura sulcicollis, A. borealis, A. standfussi, Capnia atra, Siphonoperla burmeisteri* (Benedetto 1973), *Neoperla clymene* (Vaught and Stewart 1974), *Megarcys signata* (Cather and Gaufin 1975), and *Pteronarcella badia, Skwala parallela, Diura knowltoni, Isoperla fulva, I. patricia, Sweltsa coloradensis, Suwallia pallidula*, and *Zapada columbiana* (Stanford 1975) exhibit slow cycles, with most growth occurring at moderate to warmest seasonal water temperatures. Temperature compensation (Cummins 1974) is thus manifested in this species through rapid winter growth, early spring emergence, and diapause for protection against drying or lethal temperatures in summer. This growth pattern is a selective advantage in allowing avoidance of competition for food and space with such species as *Corydalus cornutus* (Brown 1974) and *Perlesta placida*.

First instar nymphs were obtained from egg-hatching experiments and Clear Creek. They were unpigmented, had 9 antennal and 4 cercal segments, and the mean interocular distance was 0.18 mm (Fig. 5). Hynes (1976) indicated that many first-instar Plecoptera exhibit these characters.

Distinctive color patterns became evident through the middle and later instars, and numbers of cercal and antennal segments increased to 30 and 50, respectively. Mouthparts of first-instar nymphs are shown in Fig. 6. Life cycle studies of stoneflies should give attention to good descriptions of first instars to facilitate accurate identifications

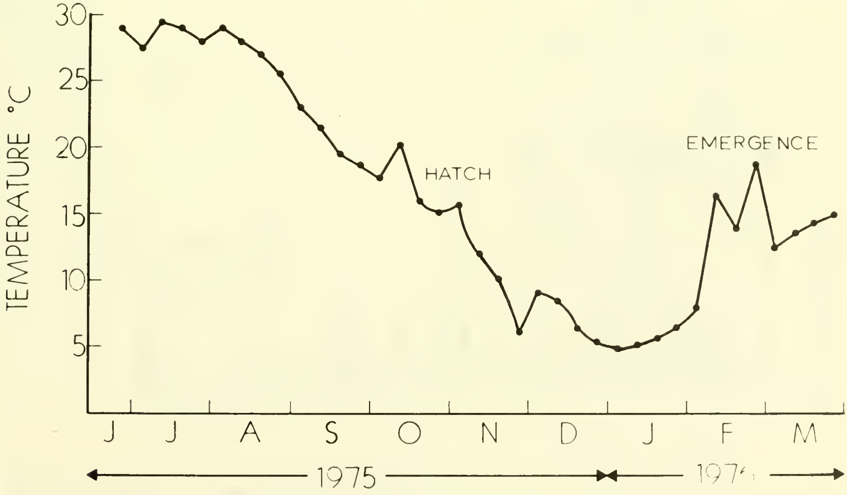

Fig. 4. Mean weekly stream temperature, June 1975 to March 1976.

for future ecological studies. Comparison of Figs. 6 and 7 show the major changes that take place in presence and pattern of setal arrangement and shape of mouthparts between first and last instars; number of palpal segments remain unchanged.

Nymphs can first be sexed at the sixth instar, by differences in the posterior setal arrangement of the eighth abdominal sternum. The fringe is interrupted in females and continuous in males. Dimorphism in setal arrangement, nymphal size, and even eventual presence of the male epiproct, becomes more distinct in postsixth instars. The sex ratio of 870 postfifth instar nymphs sexed throughout the study was 1.0 ♂ :1.1 ♀ . The larger size of female nymphs appears typical of all stoneflies and has been reported by Holdsworth (1941a, b), Heiman and Knight (1970), Tarter and Krumholz (1971), Brittain (1973), and Vaught and Stewart (1974).

Estimation of nymphal instar number was determined from 971 field-collected nymphs by using a size-frequency histogram (Fig. 8) and the methods of Cassie (1954) and Janetschek (1967) (Figs. 9 and 10, respectively). An expanded discussion of application of these methods is given by Harper (1973b) and McClure and Stewart (1976). These methods indicated 12 and up to 14 instars for males and females, respectively. Similar dimorphism in instar number has been reported by Holdsworth (1941b), McDiffett (1970), and Vaught and Stewart (1974). The size change between most instars was confirmed and these estimates substantiated by rearing field-collected nymphs of various sizes through at least one molt. Of course,

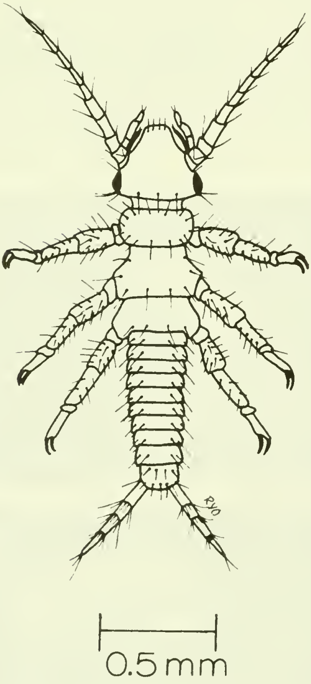

Fig. 5. *Hydroperla crosbyi* first instar nymph.

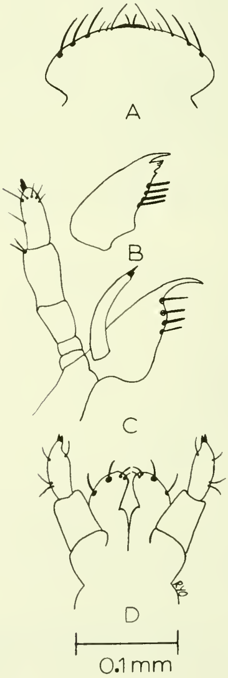

Fig. 6. *Hydroperla crosbyi* first instar nymphal mouthparts: A = labrum, B = mandible, C = maxilla, D = labium.

absolute determination of instars can only be made through rearing individuals from egg to adult, under various physical conditions (Harper 1973b). Stanford (1975) suggested that temperature may influence the number of instars in hemimetabolous insects.

Seasonal food habits of nymphs are shown in Table 2. All calculations are based on numbers of dietary items in the foregut and environment. Gut contents were examined using methods of Richardson and Gaufin (1971), and food availability was calculated from quantitative samples. Larvae of Simuliidae and Chironomidae always made up over 85 percent of the diet (Table 2), and electivity (Ivlev 1961) and forage ratio (Hess and Swartz 1941) consistently indicated that these organisms were preferred or more available. Nymphs of *Isonychia sicca manca* were the third most common dietary item, but preference for them was always negative (or they were less available

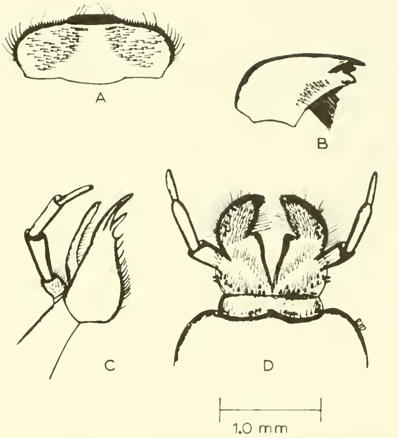

Fig. 7. *Hydroperla crosbyi* last instar female nymphal mouthparts: A = labrum, B = mandible, C = maxilla, D = labium.

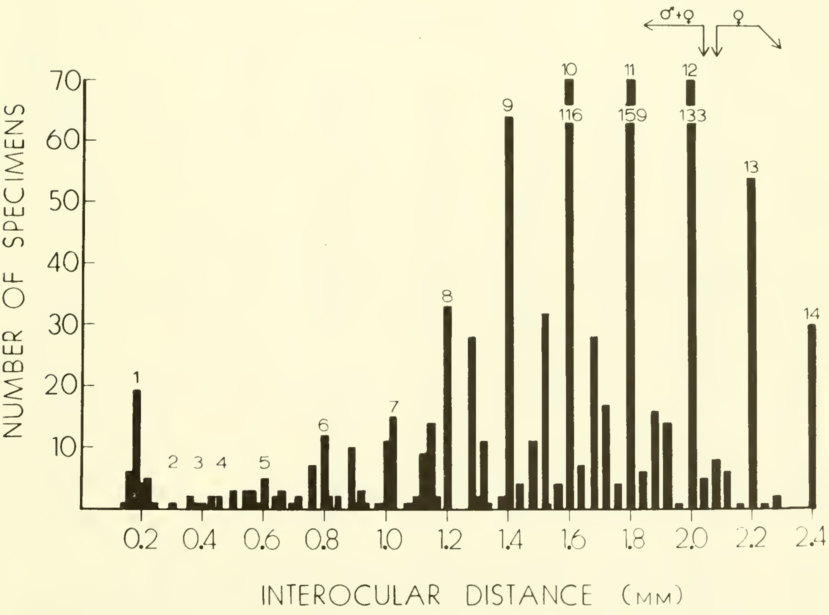

Fig. 8. Interocular distance—frequency of 971 *Hydroperla crosbyi* nymphs, illustrating instars.

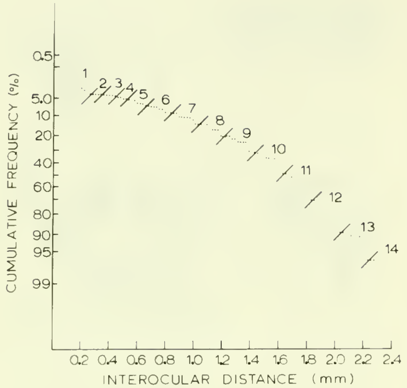

Fig. 9. Instar analysis of 971 *Hydroperla crosbyi* nymphs by Cassie (1954) method.

for feeding). *Drusinus* (Limnephilidae), *Chimarra* (Philopotamidae), *Perlesta* (Perlidae), and unidentified aquatic Lepidoptera occasionally appeared in stomachs but were considered of little importance. Frison (1935) reported large numbers of chironomids in the diet of *H. crosbyi* nymphs. Similar preferences for dipteran larvae have been reported for carnivorous insects (Minshall and Minshall 1966, Tarter and Krumholz 1971, Sheldon 1972, Stewart et al. 1973, Vaught and Stewart 1974, and Cather and Gaufin 1975). Simuliids were predominant to chironomids in the diet from November-January, with electivity or preference greater until January (Table 2). A shift in dietary occurrence became evident in February, with the two components occurring in equal proportions, then simuliids again predominated in March; electivity for sim-

TABLE 2. Seasonal food habits of 110 *Hydroperla crosbyi* nymphs November 1975 to March 1976, Clear Creek, Denton County, Texas.

		Food organisms					
		Chironomidae	Simuliidae	Baetidae *Isonychia*	% Unidentifiable	% Empty	Number examined
	% of Diet	17.2	72.4	10.3			
Nov.	% of Env.	9.2	6.6	17.6			
1975	E	0.30	0.83	0.26		0.0	9
	FR	1.87	10.97	0.58			
	% of Diet	13.6	84.1	1.1			
Dec.	% of Env.	8.3	16.4	15.0			
1975	E	0.24	0.67	0.86		16.0	25
	FR	1.64	5.13	0.07			
	% of Diet	21.0	77.2	1.7			
Jan.	% of Env.	6.9	42.1	10.0			
1976	E	0.50	0.29	0.71		11.1	27
	FR	3.04	1.83	0.17			
	% of Diet	42.8	42.8	8.3			
Feb.	% of Env.	22.9	17.2	13.2			
1976	E	0.30	0.43	-0.23	3.7	13.3	30
	FR	1.87	2.49	0.63			
	% of Diet	28.2	70.0				
Mar.	% of Env.	25.0	9.5				
1976	E	0.06	0.76			21.0	19
	FR	1.13	7.37				

uliids was greater in both these months even though in February their numbers were decreasing because of emergence. Proportion of empty stomachs was highest just prior to emergence (Table 2). Molting nymphs always had empty stomachs. Similar findings were reported by Hanson (1960), Tarter and Krumholz (1971), and Cather and Gaufin (1975). Fat stores are probably relied on for necessary energy from one to five days prior to emergence and for transformation. Finni (1975) reported preemergent fat reserves for *Allocapnia granulata*.

Mean nymphal standing crops were 8.0,

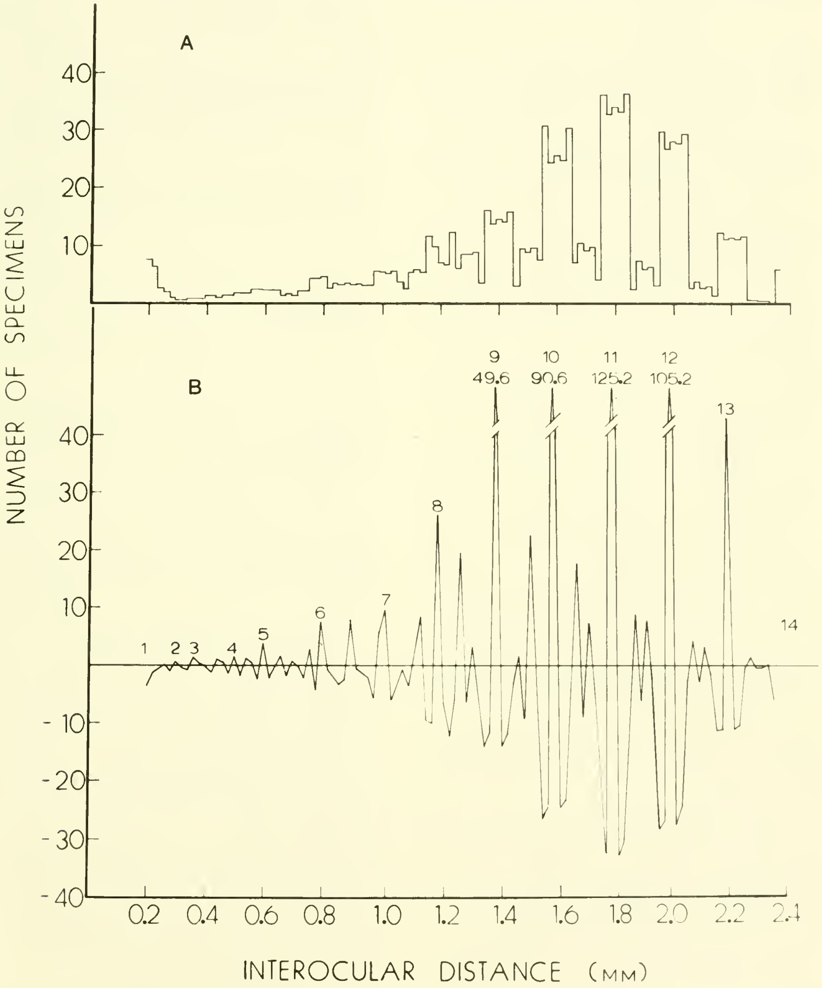

Fig. 10. Instar analysis of 971 *Hydroperla crosbyi* nymphs by Janetschek (1967) method: A = running mean of five of the frequencies, B = modal periodicity of instars (difference between Fig. 8 histogram and A).

25.6, 40.0, and 21.3/m² each month from December 1975 to March 1976. The lower number in December was probably due to sampling error, peculiarities in microdistribution, or difficulty in detection of tiny first-instar nymphs. Decreases from February-March were likely an indication of survivorship and emergence.

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SPRING WATERFOWL MIGRATION IN THE UINTA BASIN OF NORTHEASTERN UTAH

Mary E. Sangster[1]

ABSTRACT.— Spring waterfowl migrations at Ouray National Wildlife Refuge and Pelican Lake, Uintah County, Utah, were monitored during 1975 and 1976. Peak numbers occurred during the first week in April 1975 when 11,440 birds were counted. In 1976 the highest count, 9,650 birds, was made on 15 March. Most numerous early-season migrants were Mallards and Pintails. Important midseason migrants included Blue-winged and Cinnamon Teal, Canvasbacks, and Redheads. Late season migrants were Gadwall and Ruddy Ducks. Surveys conducted only at Ouray Refuge or at Pelican Lake would not adequately have reflected species composition of spring migration. Results point up the advisability of sampling large open water areas to obtain a representative view of waterfowl species composition in a given area during spring migration.

The Unita Basin, situated in northeastern Utah, is a structural depression lying between the Uinta Mountains to the north and the Tavaputs Plateau to the south. The basin is dissected by many streams and gulleys and the topography is broken and rough. Climate of this area is arid, with light snowfall and an average precipitation of less than 18 cm. Winters in the Uinta Basin are long and severe, with temperatures often falling below −18° C. Summers are short and cool and, although temperatures of 38° C are common, such temperatures do not last for prolonged periods.

The Green River transects the Uinta Basin from north to south and is the master stream for the entire drainage system of the basin. The Green River has long been known to serve as an important migratory route for waterfowl. From the south the main migratory routes follow the Colorado River to its junction with the Green. Waterfowl continue along the Green River through the Book Cliffs and the Uinta Mountains and then into Wyoming. To the west, the Provo River provides a passage from the western section of the Uinta Basin. Low passes through the Wasatch Mountains create routes into the Great Salt Lake drainage system (Twomey 1942).

In his paper on Colorado River Basin birds, Hayward (1967) stated that migrating waterfowl formerly depended almost entirely on the Green River and its tributaries for resting and feeding. More recently, Hayward noted, reservoirs constructed to produce electric power or for storage of irrigation waters have become important areas for migrating birds.

The purpose of this paper is to present information on the species and numbers of waterfowl migrating through the Uinta Basin and the chronology of spring migration in 1975 and 1976. Waterfowl counts were conducted at weekly intervals in 1975 and at 10-day intervals in 1976 from 5 March through 17 May. Waterfowl counts were made on Ouray National Wildlife Refuge in the southeast portion of the Uinta Basin. The 4,860 ha refuge is situated astride the Green River for 12 km. There are six separate bottoms along the length of the refuge which have been formed by ancient oxbows in the river. A system of shallow ponds and marshes has been constructed in these bottoms, and water pumped from the river fills these impoundments in the spring and fall. Vegetative zones on the refuge are components of the Mixed Desert Shrub Community (Twomey 1942). Waterfowl censuses were also made at Pelican Lake, a reservoir designed for irrigation of adjacent lands, located 1.6 km west of the refuge. This paper documents in detail the use of this newly created reservoir and Ouray Refuge impoundments by waterfowl of the Uinta Basin.

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The migration data presented here were collected as part of a larger study of ecology of waterfowl on Ouray National Wildlife Refuge (Sangster 1976). The study was supported by the Gaylord Memorial Laboratory (School of Forestry, Fisheries and Wildlife, University of Missouri, cooperating with the Missouri Department of Conservation) and by the Missouri Cooperative Wildlife Research Unit (U.S. Fish and Wildlife Service, Wildlife Management Institute, Missouri Department of Conservation, and the University of Missouri—Columbia cooperating). The author was an Edward K. Love Fellow. I thank Leigh H. Fredrickson for guidance and criticism during this study and Thomas S. Baskett for critically reviewing this manuscript.

Results

A few Canada Geese[2] and Mallards winter along the Green River as long as some open water is present. As more open water becomes available in March, ducks and geese begin moving into the Basin. In 1975 open water appeared at the edges of Pelican Lake the last week in February, and on 5 March a concentration of 2,500 ducks, mostly Mallards and Pintails, marked the beginning of spring migration. On 5 March 1975, pumps started moving water into impoundments on the refuge, and a week later over 2,000 birds were recorded using the refuge. In 1976 open water conditions were considerably different in the Uinta Basin due to prolonged cold weather. Pelican Lake was frozen except for a few small openings at the edge until 1 April, and refuge pumps did not begin filling the impoundments until April. Most of the early migrants in March 1976 were recorded on the Green River.

The spring migration peak in 1975 occurred during the first week in April when 11,440 birds were counted. In 1976 the highest count, 9,650 birds, was made on 15 March.

Early migrants.—Early migrants were Mallards and Pintails, which reached peak numbers during the fourth week in March 1975 and two weeks earlier in 1976 (see Table 1 for peak migration numbers and dates for all species). The peak for American Green-winged Teal was recorded the last week in March in both years, although in 1975 a second high was witnessed the second week in April. The American Wigeon, another early migrant in 1975, was most common during the third week in March. In 1976 peak numbers of wigeon occurred the second week in May. In 1975 over 75 percent of the wigeon observed were on Pelican Lake. The fact that Pelican Lake was frozen until April the following year may account for the high numbers of wigeon observed later in the season in 1976.

Midseason migrants.—Midseason migrants included Blue-winged Teal, Cinnamon Teal, Canvasback, Redhead, Bufflehead, and Shoveler. Small numbers of Lesser Scaup, Common Goldeneye, Ring-necked Ducks, and Common Merganser also were present at midseason.

In 1975 peak numbers of Cinnamon Teal, Blue-winged Teal, Canvasback, Bufflehead, Ring-necked Ducks, and Common Merganser were recorded during the second week in April and the Common Goldeneye during the third week of April. In 1976 Blue-winged Teal peaked during the same period but the peaks for the other species varied. The highest numbers of Bufflehead, Ring-necked Ducks, and Common Goldeneye were recorded the fourth week in March and Canvasback and Common Merganser were most common the first week in April. Cinnamon Teal numbers remained low until 1 May 1976.

Redhead and Lesser Scaup populations were highest during the third week in April 1975. In 1976 Lesser Scaup peaked at the same period, but peak numbers of Redheads occurred the first week in April. In 1975 Shoveler populations showed two peaks, one the third week in April and the other the first week in May. The first week in May was also a peak period for Shoveler populations in 1976.

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[2] All scientific names of waterfowl according to the American Ornithologists' Union (1957, 1973) are presented in Table 1.

LATE-SEASON MIGRANTS.—The Gadwall and Ruddy Duck were late migrants to the Uinta Basin. The Gadwall and Ruddy Duck reached peak numbers the fourth week in April 1975 and the first week in May 1976. Some Gadwall were in the area as early as the end of March but the Ruddy Duck did not appear until the second week in April. Over 85 percent of all Ruddy Ducks were observed at Pelican Lake. In 1975 a total of 1,610 Ruddy Ducks were counted, but in 1976 only 178 were observed (Tables 2 and 3). Although there were two more census periods in 1975 than in 1976, this did not appear to account for the great differences in observed numbers of migrating Ruddy Ducks through the Uinta Basin.

CANADA GEESE.—Large flocks of Canada Geese do not appear to use the Green River as a migration route. In 1975 the highest concentration of geese, 265 birds, occurred on 14 March. On 15 March 1976 a peak number of 500 geese was recorded. Other weekly census figures fluctuated between 100 and 160 geese. I believe these counts represent resident geese along the Green River. Refuge records (1965–1972) show that the average peak concentrations of geese in the spring has been 180 birds. Data for 1975 and 1976 appear to be consistent with refuge records.

Band recovery information for Canada Geese banded and released at Ouray Refuge in March 1965 yielded information on the movements of 25 birds. Of the 15 birds recovered, 12 were recovered in the Uinta Basin and 3 along the lower Colorado River. Reports on 10 birds came from retrapping information at Wheatland Reservoir in southeast Wyoming. Records for geese trapped at Wheatland Reservoir during June banding operations indicate that birds using the Ouray Refuge may move to Wyoming reservoirs to molt (unpublished records, Ouray National Wildlife Refuge). Trautin and Low (1975) proposed that the harvest of geese in northeastern Utah is dependent upon out-of-state-produced birds because the ratio of out-of-state-banded birds to Utah-banded birds is 9.00:1.00. Most of the birds banded out of state have come from Wyoming, where they were banded as molting adults. The production areas that these geese came from is un-

TABLE 1. Peak numbers and the dates recorded for migrating waterfowl in 1975 and 1976. Data for Ouray National Wildlife Refuge and Pelican Lake are combined.

Species	1975 Peak Number	1975 Peak Date	1976 Peak Number	1976 Peak Date
Mallard (*Anas platyrhynchos*)	3,725	3/28	4,750	3/15
Pintail (*Anas acuta*)	4,930	3/28	4,120	3/15
Gadwall (*Anas strepera*)	1,110	4/24	285	5/1
Shoveler (*Anas clypeata*)	635	4/16	255	5/1
American Green-winged Teal (*Anas crecca*)	775	3/28	805	3/24
Cinnamon Teal (*Anas cyanoptera*)	365	4/9	225	5/1
Ruddy Duck (*Oxyura jamaicensis*)	405	4/23	80	5/1
Canada Goose (*Branta canadensis*)	265	3/14	500	3/15
Redhead (*Aythya americana*)	315	4/16	530	4/2
American Wigeon (*Anas americana*)	345	3/20	225	5/11
Bufflehead (*Bucephala albeola*)	345	4/9	215	3/24
Lesser Scaup (*Aythya affinis*)	275	4/16	300	4/21
Common Merganser (*Mergus merganser*)	330	4/9	130	4/2
Blue-winged Teal (*Anas discors*)	175	4/9	120	4/11
Canvasback (*Aythya valisineria*)	175	4/9	140	4/2
Ring-necked Duck (*Aythya collaris*)	145	4/9	215	3/24
Common Goldeneye (*Bucephala clangula*)	90	4/16	124	3/24
Snow Goose (*Chen caerulescens*)	17	3/14	---	---
Whistling Swan (*Olor columbianus*)	---	---	50	3/15

known, but the limited band recovery data from Ouray Refuge indicate that some of these out-of-state-banded birds may actually be geese produced in the Uinta Basin.

OTHER SPECIES.—On 14 March 1975, 17 Snow Geese were sighted on Pelican Lake. Snow Geese are considered rare in the Uinta Basin (Hayward 1967).

In 1976 100 Whistling Swans were recorded during four census periods in March and April. Hayward (1967) lists this species as an uncommon transient in the upper Colorado River Basin.

American Coots (*Fulica americana*) were the most abundant migrant recorded in 1975 and 1976. Peak migration levels for coots in 1975 occurred the third and fourth weeks of April, with counts of over 6,000 birds each week. In 1976 peak numbers of coots were recorded the third week in April and the second week in May, with counts of approximately 4,500 birds.

SPECIES COMPOSITION AND LOCAL DISTRIBUTION.—During spring migration, Mallards comprised 28.9 percent of the migratory population in 1975 and 33.0 percent in 1976; Pintails 25.2 percent and 27.2 percent; teal 10.8 percent and 13.3 percent; Gadwall 8.1 percent and 4.1 percent; Shovelers 6.3 percent and 2.5 percent; and Canada Geese 3.0 percent and 4.6 percent (Tables 2 and 3). Over 80 percent of the waterfowl recorded in 1975 and 1976 were dabbling ducks.

Waterfowl use of river bottom marsh and reservoir habitat was nearly equal in 1975 but species use varied widely (Table 3). The open water of Pelican Lake was used extensively for feeding and resting by diving ducks, especially Canvasbacks, Redheads, Ruddy Ducks, Bufflehead, and American Goldeneye, as well as by wigeon and coots. In 1976 the reduced use of Pelican Lake by migrating waterfowl is readily apparent (Table 3). This can be partially explained by the frozen condition of the lake throughout March and high winds in April that made the lake less attractive to migrating waterfowl. These conditions should not have affected the numbers of late arriving migrants such as Gadwall, Ruddy Ducks, Shovelers, and Buffleheads. Apparently the riparian

TABLE 2. Comparison of species composition at Ouray National Wildlife Refuge and Pelican Lake and species composition for Ouray NWR and Pelican Lake combined, spring 1975.

Species	Ouray NWR Number	Ouray NWR Percent of Total	Pelican Lake Number	Pelican Lake Percent of Total	Combined Number	Combined Percent of Total
Mallard	7,560	33.7	6,155	24.7	13,715	28.9
Pintail	4,435	19.8	7,520	30.2	11,955	25.2
Gadwall	1,470	6.6	2,350	9.4	3,820	8.1
Shoveler	1,060	4.7	1,930	7.7	2,990	6.3
American Green-winged Teal	1,960	7.7	575	2.3	2,535	5.4
Cinnamon Teal	1,430	6.4	405	1.6	1,835	3.9
Ruddy Duck	210	0.9	1,430	5.8	1,640	3.5
Canada Goose	1,060	4.7	350	1.4	1,410	3.0
Redhead	465	2.1	880	3.5	1,345	2.8
American Wigeon	305	1.4	980	3.9	1,285	2.7
Bufflehead	310	1.4	810	3.3	1,120	2.4
Lesser Scaup	285	1.3	745	3.0	1,030	2.2
Common Merganser	970	4.3	35	0.1	1,005	2.1
Blue-winged Teal	560	2.5	140	0.6	700	1.5
Canvasback	105	0.5	300	1.2	405	0.8
Ring-necked Duck	230	1.0	150	0.6	380	0.8
Common Goldeneye	10	tr.	150	0.6	160	0.3
Snow Goose	---	---	17	0.1	17	0.1
TOTAL	22,425	100.0	24,922	100.0	47,347	100.0

TABLE 3. Comparison of species composition at Ouray National Wildlife Refuge and Pelican Lake and species composition for Ouray NWR and Pelican Lake combined, spring 1976.

	Ouray NWR		Pelican Lake		Combined	
Species	Number	Percent of Total	Number	Percent of Total	Number	Percent of Total
Mallard	8,775	38.9	275	5.6	9,050	33.0
Pintail	6,810	30.2	665	13.5	7,475	27.2
Gadwall	885	3.9	240	4.9	1,125	4.1
Shoveler	505	2.2	170	3.5	675	2.5
American Green-winged Teal	1,685	7.5	500	10.2	2,185	8.0
Cinnamon Teal	935	4.1	75	1.5	1,010	3.7
Ruddy Duck	40	0.2	140	2.9	180	0.6
Canada Goose	1,265	5.6	1	tr.	1,265	4.6
Redhead	45	0.2	875	17.8	920	3.3
American Wigeon	510	2.3	50	1.0	560	2.0
Bufflehead	120	0.5	380	7.7	500	1.8
Lesser Scaup	20	0.1	670	13.6	690	2.5
Common Merganser	335	1.5	25	0.5	360	1.3
Blue-winged Teal	405	1.8	50	1.0	455	1.6
Canvasback	55	0.2	240	4.9	295	1.1
Ring-necked Duck	80	0.4	345	7.0	425	1.5
Common Goldeneye	---	---	215	4.4	215	0.8
Whistling Swan	100	0.4	---	---	100	0.4
TOTAL	22,570	100.0	4,916	100.0	27,485	100.0

habitat of Ouray Refuge compensated for the lack of open water on Pelican Lake for the early migrants. Mallard and pintail peaks were similar both years, but the distribution between the refuge and Pelican Lake varied (Tables 1, 2, and 3).

A migration survey only at Ouray Refuge or only at Pelican Lake would not have presented a complete picture of the species composition of the spring migration. These differences in waterfowl species distribution indicate the advisability of sampling large, open water areas to obtain the species composition of the migration population for any given area.

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UTAH FLORA: BRASSICACEAE (CRUCIFERAE)

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Abstract.— The mustard family, Brassicaceae (Cruciferae) is revised for the state of Utah. Treated are 155 species and 44 varieties, including 37 species of introduced weeds or escaped cultivated plants. A key to the genera and species is included, along with detailed descriptions, distribution data, and pertinent comments for many of the taxa. Proposed new varieties are: *Lepidium montanum* Nutt. var. *stellae* Welsh & Reveal; *L. montanum* var. *neeseae* Welsh & Reveal; *Lesquerella hemiphysaria* Maguire var. *lucens* Welsh & Reveal; *Physaria acutifolia* Rydb. var. *purpurea* Welsh & Reveal; and, *Thelypodium sagittatum* (Nutt.) Endl. in Walp. var. *vermicularis* Welsh & Reveal. The following new combinations are made: *Arabis confinis* S. Wats. var. *interposita* (Greene) Welsh & Reveal; *Descurainia pinnata* (Walt.) Britt. var. *paysonii* (Detl.) Welsh & Reveal; *D. richardsonii* (Sweet) O. E. Schulz var. *brevipes* (Nutt.) Welsh & Reveal; *Draba asprella* Greene var. *zionensis* (C. L. Hitchc.) Welsh & Reveal; *Draba densifolia* Nutt. ex Torr. & Gray var. *daviesiae* (C. L. Hitchc.) Welsh & Reveal; *Lesquerella alpina* (Nutt.) S. Wats. var. *parvula* (Greene) Welsh & Reveal; *Lesquerella kingii* S. Wats. var. *parvifolia* (Maguire & Holmgren) Welsh & Reveal; *Rorippa islandica* (Oed.) Borbas var. *glabra* (O. E. Schulz) Welsh & Reveal; *Thelypodiopsis divaricata* (Rollins) Welsh & Reveal; *Thelypodium integrifolium* (Nutt.) Endl. var. *affine* (Greene) Welsh & Reveal.

This paper, dealing with the Brassicaceae, is one of a series of proposed revisions which will result ultimately in a definitive treatment of the flora of Utah. Not since the work of Tidestrom (1925) has the family been treated in its entirety, although a partial treatment is to be found in the work by Welsh and Moore (1973). The family has not been neglected by monographers, however. That observation is supported by the numerous references listed following the generic descriptions in the taxonomic treatment.

The family is both large and taxonomically complex. In the present treatment, some 199 taxa are recognized as occuring (or probably occuring) in Utah. There are 155 species and 44 varieties. Adventive weedy species and cultivated plants known to escape and persist constitute 37 species and two varieties. Thus, almost 20 percent of the taxa included are introduced. It is unlikely that any of the other large families of vascular plants in Utah, such as Asteraceae, Poaceae, Fabaceae, or Rosaceae will contain such a large proportion of weedy and adventive taxa.

Generic limits in this family are often difficult to define, and because of this well-known problem, some taxa have been shifted from one genus to another, or even among several genera, depending on the authority one chooses to follow. One author, Krause, writing in Sturm's *Flora von*

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Deutchland in 1902, proposed an inclusive genus, *Crucifera,* for plants treated in this paper as belonging to *Conringia, Diplotaxis, Erysimum, Brassica, Lepidium, Hesperis, Draba, Barbarea, Hutchinsia, Raphanus, Sisymbrium,* and *Thlaspi.* Such an approach is even more frustrating than treating taxa with obscure taxonomic limits; it is neither realistic nor is it practical.

In the Utah flora, problems of generic limits fall mainly within the purportedly primitive members of the family, such as *Streptanthus, Thelypodium, Thelypodiopsis, Caulanthus, Chlorocrambe,* and *Sisymbrium.* The approach taken herein is somewhat conservative, as we have tended to accept the various genera which appear to be more or less distinct, not only in Utah, but in other western states as well. Even so, the species treated in *Caulanthus* do not appear to represent a natural group, and some species of *Thelypodiopsis* appear to be more closely related to taxa in other genera, especially in *Thelypodium,* than they are to each other. The species in *Caulanthus* seem to show affinities to *Thelypodium, Thelypodiopsis, Chlorocrambe,* and *Streptanthus.*

In large part, we have tended to follow the published opinions of Dr. Reed C. Rollins of Harvard University, long-time student of the family, but we feel that much more work is needed in ascertaining relationships and hope that students will investigate some of the more difficult elements in the future. Some solutions might be forthcoming from studies of fine structure in various morphological features of the species, especially those to be derived from pollen morphology, from a review of phytochemistry beyond that which has already been done, and from a detailed review of cytology of the troublesome genera.

Continued reliance upon floral and fruiting characteristics, features upon which taxa have been and are currently based, is a part of the problem of arriving at a realistic system of classification of genera. An entity represents the sum of its features; yet in the Brassicaceae, much emphasis, sometimes to the exclusion of other features, has been placed on features of flowers and fruit, and, until work is directed toward an attempt to summarize all features, our understanding of the genera in this family will remain confused.

Genera and species, in the present treatment, are arranged alphabetically. The key to genera is divided into seven different, morphologically based subkeys. These artificial subkeys provide leads to groups of species or individual taxa within the various genera.

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BRASSICACEAE Burnett
Mustard Family

Annual to perennial herbs or rarely suffrutescent, often with a pungent watery juice, glabrous to pubescent with simple or more commonly branched to stellate hairs, often glaucous; leaves alternate or basal and still alternate, entire or lobed, simple to compound, exstipulate, the cauline leaves usually sessile and auriculate; flowers perfect, regular or nearly so, hypogynous, borne in ebracteate or rarely bracteate racemes, spikes, or corymbs, rarely solitary and terminal on leafless scapes; sepals 4, erect to somewhat spreading, greenish to colored, the outer 2 often somewhat bulged or saccate at the base; petals 4, rarely lacking, yellow, white, or pink to blue or purple, commonly clawed, the blade rounded to occasionally bilobed and spreading in the form of a cross (hence Cruciferae); stamens 6 with the outer 2 inserted lower and shorter than the other 4 (tetradynamous), rarely 4 or 2; nectar glands commonly 4; ovary superior, 2-loculed or, less commonly, only 1-loculed, usually with a thin partition (replum) between the two marginal placentae from which, when mature, the valves usually separate, the stigma rather small, entire to shallowly 2-lobed; fruit usually nonstipitate but occasionally so with a slender stipe, typically dehiscent or if indehiscent then constricted between the seeds (torulose) and sometimes breaking transversely, several times longer than broad (silique) to much shorter and not more than 2 or 3 times as long as broad (silicle), the sides flattened or compressed parallel with the replum or, less commonly, flattened contrary to the replum; seeds (1) 2 to several in a single row per locule (uniseriate) or more or less distinctly arranged in 2 rows (biseriate), smooth to striate or pitted and plump to flattened or even wing margined, exalbuminous.

A large, worldwide family of perhaps 375 genera and 3000 species, with many plants of economic value as ornamentals, important vegetables, or noxious weeds.

1. Plants with cauline leaves both sessile and auriculate (at least some), or auriculate and petiolate (in some *Barbarea*, *Nasturtium*, and *Rorippa*) 2
   Plants without cauline leaves or with cauline leaves not auriculate and sessile, either petioled or merely sessile 4

2(1). Petals yellow; plants glabrous or with simple hairs, rarely with some malpighian hairs in *Thelypodiopsis* .... Key I
   Petals white, pink, lavender, chestnut, or purple, but not yellow (cream colored in *Camelina* and *Arabis*); plants glabrous or variously pubescent 3

3(2). Plants glabrous or with simple trichomes only .... Key II
   Plants pubescent with at least some malpighian, branched, or stellate hairs .... Key III

4(1). Petals yellow, sometimes fading white or pinkish to purplish 5
   Petals white, pink, lavender, purple, or chestnut, but not yellow 6

5(4). Plants glabrous or with simple hairs only .... Key IV
   Plants pubescent with malpighian, branched, or stellate hairs .... Key V

6(4). Plants glabrous or with simple hairs only .... Key VI
   Plants pubescent with at least some malpighian, branched, or stellate hairs .... Key VII

KEY I

Cauline leaves auriculate; petals yellow

1. Uppermost cauline leaves falsely perfoliate-clasping; basal leaves finely dissected, usually lacking at anthesis; seeds 2, one in each locule; silicles about as broad as long (*L. perfoliatum*) .... *Lepidium*
   Uppermost cauline leaves various, but not perfoliate-clasping, more than twice as long as broad; basal leaves pinnatifid to dentate or subentire; seeds several to many, or reduced to one in *Isatis*; siliques or silicles more than twice as long as broad 2

2(1). Cauline leaves lyrate-pinnatifid or falsely petiolate above the auriculate base 3
   Cauline leaves entire, ovate to oblong or lanceolate, undulate or rarely toothed, sessile 4

3(2). Styles (0.5) 1-2 mm long, abruptly contracted at the stigma; fruit 15 mm long or more, many times longer than broad; plants not rhizomatous .... *Barbarea*

Styles 0.5-0.8 (1.3) mm long, or if longer, then plants rhizomatous, tapering to the stigma; fruit less than 10 mm long (rarely longer), 1 to several times longer than broad .... *Rorippa*

4(2). Cauline leaves hastately lobed; pedicels deflexed in fruit; slilicles cuneate, winged-flattened 1-seeded, 1-loculed .... *Isatis*

Cauline leaves clasping-auriculate; pedicels spreading-ascending to ascending in fruit; siliques linear, not or only somewhat flattened, not winged, many-seeded, 2-loculed 5

5(4). Cauline leaves broadly rounded to truncate apically, strictly entire, elliptic-oblong to lance-oblong .... *Conringia*

Cauline leaves rounded to acute apically, more or less dentate to entire, tapering from base to apex 6

6(5). Plants biennial; weeds of cultivated or disturbed sites; basal leaves lyrate-pinnatifid (*B. campestris*) .... *Brassica*

Plants perennial or biennial, rarely annual; indigenous plants of clay soils; basal leaves dentate to entire 7

7(6). Stamens exserted; siliques long-stipitate, the stipe 1-2 cm long or more (*S. viridiflora*) .... *Stanleya*

Stamens included; siliques sessile or only short-stipitate .... *Thelypodiopsis*

KEY II

Cauline leaves auriculate; petals white, pink, lavender, or chestnut; herbage glabrous or with simple trichomes only

1. Leaves pinnately compound or pinnatifid; plants aquatic, glabrous (or nearly so); flowers white .... *Nasturtium*

Leaves simple, entire or merely toothed; plants terrestrial; flowers white, pink, lavender, or chestnut 2

2(1). Uppermost cauline leaves commonly rounded to emarginate or truncate apically, the lower ones dentate apically; flowers chestnut to brown-purple or purple; siliques 3-5 (6) mm broad .... *Streptanthus*

Uppermost cauline leaves attenuate to acute apically, the lower ones various but not apically dentate only; flowers white, pink, or lavender 3

3(2). Plants annual or winter annual; pedicels recurved in fruit; fruit indehiscent, winged-flattened, 1-seeded, 1-loculed; restricted to Washington Co. .... *Thysanocarpus*

Plants annual, biennial, or perennial; pedicels spreading-ascending to erect, rarely descending in some *Thlaspi*; fruit dehiscent or indehiscent in *Cardaria*, winged-flattened to subterete, 2 or more seeded; distribution various 4

4(3). Limb of petal 4-6 (7) mm long; sepals mostly 4-7 mm long; siliques (at least some) more than 5 cm long 5

Limb of petal 2-3 mm long or less; sepals mostly 2-4 (7) mm long; siliques or silicles less than 5 cm long except in *Arabis* 6

5(4). Petals obovate, constricted at the base, the claw broad; stigma expanded and deeply bilobed; plants of eastern Utah (*T. elegans*) .... *Thelypodiopsis*

Petals oblanceolate, tapering to a slender claw; stigma narrowed, not deeply bilobed; plants mostly of north-central and western Utah (*T. sagittatum*) .... *Thelypodium*

6(4). Fruit 10-30 times longer than broad or more, linear or narrowly oblong in outline 7

Fruit 1-4 times longer than broad or less, clavate to obcordate, ovate, or cordate-reniform in outline 9

7(6). Pedicels mostly 8-12 mm long, erect or nearly so; plants of middle altitudes in mountains (*A. hirsuta*) .... *Arabis*

Pedicels 2-7 mm long, spreading-ascending to descending; plants of low to moderate elevation 8

8(7). Plants 10 dm tall or more, biennial, the basal leaves often withered at anthesis; cauline leaves numerous, somewhat hastately and acutely auriculed; known only from central northern Utah (*T. rollinsii*) .... *Thelypodium*

Plants 4 dm tall or less, annual or winter annual, the basal leaves not withered at anthesis; cauline leaves few to several, cordate-auricled to merely sessile; known only from Washington Co. (*C. cooperi*) .... *Caulanthus*

9(6). Seeds and ovules 3 to many per fruit, usually 2 or more in each locule; fruit conspicuously winged or more than twice as long as broad .... *Thlaspi*

Seeds and ovules 2 per fruit, 1 in each locule; fruit not or only somewhat winged 10

10(9). Fruit broader than long, indehiscent; upper cauline leaves ovate; racemes 2-5 cm long in fruit, numerous .... *Cardaria*

Fruit longer than broad, dehiscent; upper cauline leaves lanceolate; racemes 5-10 cm long or more in fruit, few (*L. campestre*) .... *Lepidium*

KEY III

Cauline leaves auriculate; petals white, pink, or lavender,
(except in *Camelina* and *Arabis*); herbage pubescent
with malpighian, branched, or stellate hairs

1. Plants indigenous biennials or perennials of broad distribution in native plant communities; fruits siliques, several to many times longer than broad; flowers pink, lavender, or white (cream in *Arabis glabra*) 2

Plants adventive annuals or winter annual of disturbed or cultivated places; fruits silicles, less than 3 times longer than broad; flowers usually white 3

2(1). Plants pubescent with mixed simple, forked, and branched hairs; siliques subquadrangular; known only from the northern foothills of the Uinta Mts. .... *Halimolobos*

Plants variously pubescent but not as above nor of that distribution; siliques distinctly flattened .... *Arabis*

3(1). Plants flowering in early springtime; siliques triangular-obcordate, compressed .... *Capsella*

Plants flowering in late springtime and summer; siliques obovoid, terete or nearly so .... *Camelina*

KEY IV

Cauline leaves sessile or petiolate, not auriculate, or if hastately lobed then petiolate; flowers yellow; herbage glabrous or with simple hairs only

1. Cauline leaves both hastately lobed and petiolate, the leaf-blades triangular-ovate or lanceolate, entire; plants mostly 8 dm tall or more; of middle elevations often in dense vegetation .... *Chlorocrambe*
   Cauline leaves pinnatifid to entire, the leaf-blades not hastately lobed; plants low to tall, but if tall then seldom if ever of middle elevations in dense vegetation 2

2(1). Leaves all simple and entire or sparingly toothed; plants perennial from a caudex 3
   Leaves (at least some) pinnatifid or definitely and regularly toothed (or, if all entire, then plant not arising from a caudex); plants annual, biennial, or perennial, sometimes with a distinct caudex 6

3(2). Plants low, less than 1 dm tall; cauline leaves lacking; silicles lanceolate in outline, 1-4 times longer than broad (*D. densifolia*) .... *Draba*
   Plants 1-5 dm tall or more; cauline leaves present; siliques linear, many times longer than broad 4

4(3). Stamens long-exserted from the flower; pedicels spreading; siliques long-stipitate on stipes 10-25 mm long or more .... *Stanleya*
   Stamens not exserted beyond the flower; pedicels ascending to suberect; siliques sessile, subsessile, or on a short stipe less than 1 mm long 5

5(4). Siliques 10-20 mm long, 2-3 mm wide; plants known only from Uintah Co. .... *Glaucocarpum*
   Siliques 25-65 mm long, 0.8-1.2 mm wide; plants widespread and often weedy .... *Schoencrambe*

6(2). Plants growing in mud, along beaches, or in or near streams; petals usually less than 3 mm long; siliques usually less than 12 mm long .... *Rorippa*
   Plants seldom if ever in perennially moist sites; petals more than 4 mm long or siliques more than 12 mm long, or both 7

7(6). Leaves glaucous, thickened; perennial herbs from an often woody caudex; stamens long-exserted; siliques long-stipitate on stipes 10-25 mm long .... *Stanleya*
   Leaves not glaucous, or, if so, not especially thickened; annual, biennial, or perennial herbs without a distinct caudex (except *Schoencrambe*); stamens not exserted; siliques not stipitate 8

8(7). Plants perennial, rhizomatous, indigenous, of lower elevations in native plant communities .... *Schoencrambe*
   Plants annual or biennial, adventive, of disturbed or cultivated places 9

9(8). Fruits dehiscent to the apex; pedicels spreading-ascending to ascending, or, if erect (as in *S. officinalis*), the petals only 3-4 mm long .... *Sisymbrium*
   Fruits with long, indehiscent sterile apices; pedicels ascending, or, if appressed (as in *B. nigra*), the petals 5-8 mm long or more 10

10(9). Plants mostly 2-5 dm tall; leaves mainly basal; fruiting racemes longer than the leafy stems; seeds biseriate .... *Diplotaxis*

Plants mostly 4-10 dm tall or more; leaves basal and cauline; fruiting racemes shorter than the leafy stems; seeds uniseriate .... *Brassica*

KEY V

Plants with cauline leaves sessile or petiolate or lacking;
petals yellow; herbage pubescent with malpighian,
branched, or stellate hairs

1. Leaves once to twice or rarely thrice pinnately dissected or compound; plants annual or winter annual .... *Descurainia*
Leaves simple and entire or merely toothed or lobed; plants annual, biennial, or perennial 2

2(1). Cauline leaves lacking, all leaves basal .... *Draba*
Cauline leaves present, at least one, the basal leaves present or absent 3

3(2). Plants pubescent with appressed, Y-shaped and/or malpighian hairs; siliques many times longer than broad .... *Erysimum*
Plants pubescent with branched, dendritic, or appressed stellate hairs; silicles from about as broad as long to about 5 times longer than broad 4

4(3). Pubescence of branched or dendritic hairs, rarely with some stellate; silicles lance-ovate to oblong or elliptic, usually more than twice as long as broad .... *Draba*
Pubescence of appressed stellate hairs only (except for *Alyssum saxatile*); silicles orbicular in outline or subglobose to bladdery inflated, not over twice as long as broad 5

5(4). Silicles compressed, lens-shaped; plants annual .... *Alyssum*
Silicles either subglobose or greatly inflated and terete or didymous; plants annual, biennial, or perennial 6

6(5). Basal leaf blades often exceeding 20 mm in width; silicles (excluding style) 8-10 mm long or more, didymous and bladdery inflated, often cordate at the base .... *Physaria*
Basal leaf blades rarely up to 20 mm in width; silicles (excluding style) 3-6 mm long, not didymous, seldom bladdery inflated, not cordate at the base .... *Lesquerella*

KEY VI

Plants with cauline leaves sessile or petiolate or lacking;
petals white, pink, lavender, purple, or chestnut;
herbage glabrous or with simple hairs only

1. Herbage stipitate-glandular or glabrous and the plants scapose and with large flowers; plants either alpine perennials or winter annuals of low elevations 2
Herbage glabrous or simple hirsute; plants of various habits, habitats, and duration 3

2(1). Plants scapose alpine perennials; leaves basal; petal blades 8-10 mm long or more; siliques flattened, dehiscent .... *Parrya*
Plants winter annuals; leaves cauline and basal; petal blades 2-4 mm long; siliques terete, indehiscent .... *Chorispora*

3(1). Blades of cauline leaves hastately lobed, otherwise entire, triangular-ovate to triangular-lanceolate; plants 8-10 dm tall or more; siliques short-stipitate, the stipe 2-7 mm long .... *Chlorocrambe*

Blades of cauline leaves, if any, not both hastately lobed and entire; plants low to tall; siliques or silicles subsessile or sessile on the pedicel (except in *Lunaria*) 4

4(3). Plants dwarfed scapose perennials; leaves often less than 10 mm long; scapes often less than 10 cm tall .... *Draba*

Plants caulescent, at least some leaves cauline; leaves mostly more than 10 mm long; stems usually over 10 cm tall 5

5(4). Plants slender annuals, 1-2.5 dm tall; leaves entire or merely serrate (at least the cauline ones); fruits obovate in outline and several-seeded, or, if linear, less than 15 mm long 6

Plants annual, biennial, or perennial, 1.5-10 dm tall or more; leaves variously toothed, lobed, or entire; fruits obovate in outline and 2-seeded, or lance-ovoid, or, if linear, mostly more than 15 mm long 7

6(5). Petals 1.2 mm long or less; silicles obovate, compressed, 2-3 mm long .... *Hutchinsia*

Petals 2-2.9 mm long; siliques linear, terete, 9-14 mm long .... *Arabidopsis*

7(5). Basal leaves long-petiolate, the blades oblong to lanceolate, mostly 10-30 (50) cm long or more; cauline leaves lance-oblong, irregularly crenate-serrate; petals white; silicles less than twice longer than broad, abortive; plants cultivated but escaping and often persistent .... *Armoracia*

Basal leaves sessile, poorly developed, or if long-petiolate, the blades seldom as above, usually less than 10 cm long; cauline leaves not both lance-oblong and irregularly crenate-serrate; petals pink, white, or chestnut purple; fruit various; plants indigenous or cultivated 8

8(7). Petal blades 8-12 mm long, pink to lavender; silicles more than 20 mm wide; styles 6-8 mm long; leaves cordate-ovate, irregularly toothed .... *Lunaria*

Petal blades usually less than 8 mm long; silicles or siliques much less than 10 mm wide; styles less than 3 mm long; leaves various but not cordate-ovate (except in *Cardamine cordifolia*) 9

9(8). Seeds and ovules 2, 1 in each locule; silicles obcordate, orbicular, or elliptic, usually about as long as broad .... *Lepidium*

Seeds and ovules more than 2, usually more than 2 in each locule; silicles lance-oblong or siliques linear and 3 to many times longer than broad 10

10(9). Plants annual, with thickened tuberous roots; flowers white or pink, the petal limb more than 5 mm long; siliques terete, indehiscent .... *Raphanus*

Plants perennial, biennial, or, if annual, not from thickened roots; flowers variously colored, but if white or pink then the petal limb less than 5 mm long; siliques or silicles terete or flattened, dehiscent 11

11(10). Cauline leaves ovate, cordate-ovate, or pinnately compound; flowers white; plants of moist sites .... *Cardamine*

Cauline leaves pinnatifid or entire to subentire and linear to elliptic, but not as above; flowers white or brown-purple, lavender or with purple veins; plants of various habitats 12

12(11). Flowers minute, less than 1.2 mm long; silicles lance-oblong, less than 10

mm long; leaves lyrate-pinnatifid (*R. tenerrima*) .... *Rorippa*
Flowers 2-6 mm long or more; siliques linear to oblong, much more than 10 mm long; leaves pinnatifid to toothed or entire 13

13(12). Flowers subsessile, the pedicels less than 2 (4) mm long; leaves, at least some, definitely pinnatifid; petals mostly brown-purple .... *Caulanthus*
Flowers pedicellate, the pedicels usually over 2 mm long, or the leaves entire; petals variously colored, but, if brown-purple, pedicels definitely longer than 2 mm 14

14(13). Plants annual; pedicels curved-descending; siliques compressed, the sutures parallel, not torulose .... *Streptanthella*
Plants biennial or perennial; pedicels spreading to spreading-ascending (declined in *Thelypodium wrightii*); siliques with parallel sides or else torulose 15

15(14). Petals strongly purple-veined; leaves linear; plants from a caudex, known only from Uintah Co. (*T. argillacea*) .... *Thelypodiopsis*
Petals not or seldom purple veined; leaves various; plants with or without a caudex, of various distribution 16

16(15). Plants erect biennials; basal rosette prominent, but usually withered at anthesis; pedicels spreading or declined; siliques torulose; flowers numerous to very numerous .... *Thelypodium*
Plants ascending to erect perennials; basal rosette not especially prominent; pedicels spreading-ascending; siliques with parallel sides; flowers several to many (*A. nuttallii*) .... *Arabis*

KEY VII

Plants with cauline leaves sessile, petiolate, or lacking;
petals white, pink, lavender, or purple; herbage pubescent
with malpighian, branched, or stellate hairs

1. Leaves pinnately lobed; herbage cinereous pubescent; plants of high elevations .... *Smelowskia*
Leaves entire to serrate or sinuate-dentate; herbage green or glaucous (cinereous in *Dithyrea*); plants of low to high elevations 2

2(1). Plants scapose, the leaves basal, mostly less than 1 dm tall .... *Draba*
Plants with at least some leaves cauline, often more than 1 dm tall 3

3(2). Petal blades more than 6 mm long; sepals definitely saccate, 6-8 mm long; cauline leaves sinuate-dentate; plants 5-10 dm tall or more, cultivated and frequently escaping .... *Hesperis*
Petal blades less than 6 mm long; sepals not especially saccate, 1-6 mm long; cauline leaves entire or sinuate-dentate; plants (0.5) 1-4 dm tall, indigenous or adventive, not cultivated (except *Lobularia*) 4

4(3). Styles (1.5) 2-3 mm long; ovaries appressed stellate pubescent, about twice as long as broad, dehiscent; seeds several .... *Berteroa*
Styles 0.2-1 (1.5) mm long; ovaries variously pubescent, but if appressed stellate then much broader than long, dehiscent or indehiscent; seeds 1 to many 5

5(4). Pedicels 5-21 mm long, spreading; silicles with stellate or dendritic pub-

escence, more than twice as broad as long, 2-seeded .... *Dithyrea*
Pedicels less than 8 mm long or not spreading, or, if spreading, silicles or siliques not with stellate or dendritic hairs and broader than long; seeds 1, 2, or more 6

6(5). Petals minute, less than 2 mm long; seeds 1 or 2; fruit indehiscent; plants annual or winter annual 7
Petals mostly 2-10 mm long or more; seeds 2 to many; plants annual, biennial, or perennial 8

7(6). Ovaries and fruit with dendritic pubescence; fruit ovoid, with a curved stylar beak up to 1 mm long, 2-seeded .... *Euclidium*
Ovaries and fruit with simple hairs; fruit orbicular, compressed, lacking a stylar beak, 1-seeded .... *Athysanus*

8(6). Pedicels less than 2 mm long, appressed or ascending; leaves sinuate-dentate; siliques ascending, 33-63 mm long, pubescent with dendritic or branched hairs, the stigma oblique .... *Malcolmia*
Pedicels 2-10 mm long, descending to spreading or ascending; silicles or siliques various, sometimes pubescent with dendritic or branched hairs, the stigma terminal 9

9(8). Pedicels descending; fruit pendulous, 13-65 mm long; plants perennial .... *Arabis*
Pedicels spreading to ascending; fruit erect or spreading-ascending, 2-14 mm long; plants annual or perennial 10

10(9). Leaves mainly cauline, strigose with malpighian hairs; fruit about as broad as long; seeds 2; plants cultivated and often escaping .... *Lobularia*
Leaves mainly basal, with stalked dendritic or stellate hairs; seeds usually more than 2; plants indigenous or adventive 11

11(10). Fruit linear to narrowly oblong, terete or subterete, less than 1 mm broad; plants slender annuals .... *Arabidopsis*
Fruit lance-ovate to lanceolate or oblong in outline, flattened, 1.5-3 mm broad; plants annual or perennial .... *Draba*

ALYSSUM L.

Plants stellate-pubescent annuals or perennials from taproots; leaves alternate, simple, entire, tapering to base, not auriculate; flowers in racemes, pedicels spreading-ascending to ascending or erect, not subtended by bracts; sepals 4, deciduous or persistent; petals 4, yellow (often fading cream or white), emarginate; stamens 6, at least the two shorter filaments with a whitish process near base; style slender, stigma capitate; fruit a sessile silicle, less than twice longer than broad, broadly elliptic to oval in outline, compressed parallel to the septum, valves veinless; seeds 1 or 2 per locule.

1. Cauline leaves, at least some, more than 4 cm long; flowers bright yellow, fading cream; petal blades obcordate, about as broad as long; plants perennial, cultivated and occasionally escaping .... *A. saxatile*
Cauline leaves less than 4 cm long; flowers pale yellow (fading white); petal blades cuneate, much longer than broad; plants adventive annuals of arid sites 2

2(1). Silicles glabrous or essentially so, orbicular in outline; styles 0.5-0.8 mm long, persistent .... *A. desertorum*

Silicles stellate-pubescent, orbicular to elliptic in outline; styles various 3

3(2). Silicles 4-5 mm broad; styles 0.8-1.2 mm long; pubescence of coarse spreading-ascending stellate hairs .... *A. minus*

Silicles 2.8-4 mm broad; styles 0.3-0.6 mm long; pubescence of delicate appressed-stellate hairs 4

4(3). Silicles emarginate at the style, about as broad as long; hairs of fruit minute, not or seldom overlapping .... *A. alyssioides*

Silicles truncate at the style, longer than broad; hairs of fruit ample, usually overlapping .... *A. szowitsianum*

Alyssum alyssioides (L.) L. (*Clypeola alyssioides L.*) Alyssum. Plants annual, stems ascending to erect, simple or branched from near base (3) 6-25 cm tall; leaves spatulate to oblanceolate, 5-20 (37) mm long, 2-6 mm broad, stellate and green on both surfaces; pedicels spreading-ascending, 1.5-4 (5) mm long; sepals 2.1-2.8 (3) mm long, green, stellate-pubescent, persistent; petals 3-4.2 mm long, yellow, fading white, cuneate, surpassing sepals; silicles 3-4 mm long and about as broad, valves minutely stellate-pubescent, emarginate at style; styles persistent, mostly 0.3-0.6 mm long. Foothills, roadways, and other dry sites at low elevations in Cache, Salt Lake, Tooele, Utah, and Wasatch counties, and to be expected elsewhere; widespread in North America; adventive from Europe.

Alyssum desertorum Stapf. Desert Alyssum. Plants annual, stems decumbent to ascending or erect, simple or branched from near the base, (3) 4-20 cm tall; leaves spatulate to oblanceolate or almost linear, 4-22 mm long, 2-3 mm wide, stellate and green on both surfaces; pedicels spreading-ascending, 1.8-2.5 mm long; sepals 1.2-1.9 mm long, often suffused with red, stellate-pubescent; petals 2.3-2.8 mm long, yellow, fading white, cuneate, surpassing sepals; silicles 2.9-3.8 mm long and about as broad, valves glabrous or rarely with scattered stellate hairs, emarginate at the style; styles persistent, 0.5-0.8 mm long. Foothills, roadsides, and other dry sites at low elevations in Morgan, Salt Lake, Sanpete, Tooele, Utah, and Weber counties, and to be expected elsewhere; Washington, Oregon, Idaho, and Montana; adventive from Asia Minor and adjacent southeastern Europe (Rollins, R. C. 1941. Contr. Dudley Herb. 3: 183).

Alyssum minus (L.) Roth. (*Clypeola minor* L.). Plants annual, stems ascending to erect, simple or branched from near base, 0.9-2.5 dm tall; leaves spatulate to oblanceolate, 4-25 mm long, 2-7 mm broad, coarsely stellate and green on both surfaces; pedicels spreading-ascending, 2.8-4.9 mm long; sepals (1.5) 1.7-2.5 mm long, often suffused with red, stellate-pubescent, caducous; petals 2.7-3.6 mm long, yellow, fading white, surpassing sepals; silicles (3.5) 4-5.2 mm long and about as broad or broader, valves coarsely stellate with ascending rays, emarginate at style; styles persistent, 0.8-1.2 mm long. Foothills and roadsides in Salt Lake Co., and to be expected elsewhere; California and Colorado; adventive from the Old World.

Alyssum saxatile L. Sweet Alyssum. Annual, stems sprawling-decumbent to ascending or erect, branched from base and above, 20-35 cm tall; leaves oblanceolate to elliptic or oblong, 90-135 mm long, 2-17 mm wide, minutely stellate and with long, forked, and simple hairs, and green on both surfaces; pedicels spreading-ascending, 3.5-8 mm long; sepals 1.7-3 mm long, green or cream, loosely stellate to glabrate, caducous; petals 4-5 mm long, yellow, fading cream, much surpassing sepals; silicles 3.5-4.5 mm long or more and about as broad, valves glabrous, truncate to rounded at style; styles persistent, 0.5-1 mm long. Cultivated ornamental, occasionally escaping; introduced from southern Europe

Alyssum szowitsianum Fisch. & Meyer Szowits Alyssum. Plants annual, stems decumbent-ascending to erect, usually branched from near base, 5-15 cm tall; leaves oblanceolate, 8-25 mm long, 1-5 mm broad, stellate and green or suffused with red on both surfaces; pedicels ascending to erect, 2.7-4.2 mm long; sepals 0.9-1.2 (2) mm long, often suffused with red, stellate-pubescent, caducous; petals 1.7-2 mm long, yellow, fading white, only slightly surpassing the sepals; silicles 4-5 (6) mm long, longer than broad, valves densely stellate, truncate at style; styles persistent, 0.5-0.6 mm long. Dry foothills, in Salt Lake County, and to be expected elsewhere; adventive from Europe.

ARABIDOPSIS (DC.) Schur

Plants annual, glabrous, or pubescent with simple or branched hairs, from taproots; leaves alternate or basal (and still alternate), simple, entire, or remotely serrate, tapering to base, not auriculate; flowers in racemes, pedicels spreading-ascending, not subtended by bracts; sepals 4, deciduous; petals 4, white, not emarginate; stamens 6, at least the two shorter filaments subtended by a semicircular gland; style very short, tapering, stigma not enlarged; silique sessile, several times longer than broad, subterete, valves with conspicuous mid-nerve; seeds several to many in each locule.

Arabidopsis thaliana (L.) Schur. Mouse-ear Cress. (*Arabis thaliana* L.). Plants slender annuals, stems erect or nearly so, usually branched throughout, 8-30 (40) cm tall; leaves mainly basal, spatulate to oblong, 3-30 (50) mm long, 2-8 mm broad, remotely toothed to subentire, pubescent with simple or 2- to 4 (5) -rayed hairs, green; cauline leaves much smaller than basal ones, lance-oblong, sessile or nearly so, 5-20 mm long, 2-5 mm wide; pedicels very slender, 2.5-10 mm long; sepals 1.2-1.7 mm long, green to cream or reddish tinged, sparingly long-hairy; petals 2-2.9 mm long, white, spatulate, surpassing sepals; siliques 9-14 mm long, 0.5-0.8 mm broad, valves glabrous; styles 0.2-0.3 mm long. Dry hillsides at lower elevations in Salt Lake and Weber counties, and to be expected elsewhere; widespread in temperate North America; adventive from Europe.

ARABIS L.
Rock-Cress

Plants biennial or perennial, glabrous or pubescent with simple, branched, or stellate hairs; leaves alternate and basal, simple, entire, dentate, serrate, or sinuate, tapering to base or cauline blades sessile and usually auriculate; flowers in racemes, the pedicels erect, ascending, spreading-ascending, spreading, descending, or reflexed, not subtended by bracts; sepals 4, deciduous; petals 4, white, pink, lavender, or purple (cream in *A. glabra*); stamens 6, at least the two shorter filaments subtended by glands; styles prominent to lacking, the stigmas entire to lobed; fruit a sessile or substipitate silique many times longer than broad, laterally flattened, valves usually with a midnerve; seeds numerous.

A large genus of perhaps 100 species of Eurasia and North America.

Rollins, R. C. 1941. Monographic study of *Arabis* in western North America. Rhodora 43: 289-325, 348-411, 425-481. Reprinted at Contr. Gray Herb. 138.

1. Cauline leaves usually attenuate to rounded basally, either petiolate or sessile but not auriculate (rarely so in *A. pendulina*) 2
   Cauline leaves auriculate, at least some 6

2(1). Petals 9-18.5 mm long; petal limb divaricate; ovary and silique densely pubescent; herbage pubescent with minute dendritic hairs .... *A. pulchra*
   Petals (4.5) 5-8 (9) mm long; petal limb ascending to erect; ovary and silique glabrous or sparingly hairy only; herbage glabrous or with simple or branched hairs 3

3(2). Pedicels spreading-ascending to erect; siliques ascending to erect 4
   Pedicels divaricate to descending; siliques descending to pendulous 5

4(3). Pedicels and siliques erect; siliques 3-6 cm long; plants widespread in northern and central Utah .... *A. hirsuta*
Pedicels and siliques merely ascending; siliques 1-3 cm long; plants known only from Cache County .... *A. nuttallii*

5(4). Seeds biseriate; siliques 2-3 mm broad; plants of central and southern Utah .... *A. pendulina*
Seeds uniseriate; siliques 1.5-2 mm broad; plants of Daggett and Uintah counties .... *A. demissa*

6(1). Lower leaves and/or stems pubescent exclusively with malpighian hairs (at least some); flowers white to pink; pedicels and siliques erect; plants widespread .... *A. drummondii*
Lower leaves and/or stems glabrous or variously pubescent but not exclusively of malpighian hairs only, or, if so, otherwise various; flowers white, pink, lavender, or purple (cream in *A. glabra*); pedicels and siliques variously disposed but sometimes erect 7

7(6). Basal leaves more or less hirsute and usually ciliate with long simple or forked hairs, not both hirsute and with dendritic hairs on the blade surfaces 8
Basal leaves more or less densely pubescent with dendritic (rarely malpighian) hairs, rarely also with a few long simple or forked hairs along the leaf bases 11

8(7). Flowers cream to white or pinkish; pedicels and siliques ascending to erect 9
Flowers pink to lavender or purple, rarely white; pedicels and siliques spreading to descending 10

9(8). Stigmas expanded. 0.8-1.1 mm broad, much wider than the style base; outer sepals not gibbous at the base; petals cream to rarely pinkish; siliques not strongly compressed; plants from Utah County northward .... *A. glabra*
Stigma not obviously expanded, 0.3-0.6 mm broad, not much wider than the style base; outer sepals gibbous at the base; petals white to pink; siliques definitely compressed; plants of a broader distribution .... *A. hirsuta*

10(8). Stems solitary or few, 2.5-6 dm tall; cauline leaves 1-4 cm long; seeds biseriate .... *A. fendleri*
Stems several to many, 1-3 dm tall; cauline leaves 0.5-1 cm long; seeds uniseriate .... *A. demissa*

11(7). Fruiting pedicels (but not necessarily the siliques) ascending to erect; siliques erect to spreading or even curved-pendulous 12
Fruiting pedicels spreading to descending, pendulous, or appressed downward along the axis of the raceme 16

12(11). Leaves, stems, and pedicels (and sometimes even the siliques) hoary with minute soft hairs; plants of central western Utah .... *A. shockleyi*
Leaves variously pubescent; stems and pedicels glabrous or puberulent, or the stems hairy near the base only; plants of various distributions 13

13(12). Pedicels erect; siliques erect or steeply ascending; plants 0.5-2.5 dm tall, of alpine sites at high elevations .... *A. lyallii*
Pedicels spreading-ascending to ascending; siliques spreading to more or less pendulous; plants (2) 2.5-5 dm tall or more, of moderate to low ele vations 14

14(13). Stems usually solitary, 3-10 dm tall (usually pubescent with malpighian hairs); cauline leaves 10 or more, well developed, closely positioned, and often overlapping .... *A. confinis*
Stems usually more than one, 2.5-5 dm tall; cauline leaves usually fewer than 8, poorly developed, commonly widely spaced and only the lowermost overlapping 15

15(14). Stems arising from between the basal rosette and a tuft of ascending leaves; basal leaves mostly 2.5-5 cm long or more .... *A. selbyi*
Stems arising from the basal rosette, a secondary tuft of leaves lacking or poorly developed; basal leaves mostly 0.5-2.5 cm long .... *A. microphylla*

16(11). Lowermost leaves entire, poorly developed, smaller than the main cauline ones; cauline leaves linear to narrowly oblong; siliques more or less finely pubescent .... *A. pulchra*
Lowermost leaves in a rosette, more or less well developed, usually oblanceolate to spatulate and broader than the main cauline ones, often toothed; siliques not or rarely pubescent (except in *A. puberula*) 17

17(16). Stems usually 3 or more, arising between basal rosette and an ascending-erect tuft of leaves; lowermost leaves more or less toothed; pedicels spreading-descending; siliques more or less pendulous .... *A. perennans*
Stems usually solitary, rarely 3 or more but then branches not arising from between a basal rosette and a tuft of ascending leaves, lowermost leaves entire or toothed 18

18(17). Leaves, stems, pedicels and fruit densely pubescent with minute hairs; plants of north central and perhaps western Utah .... *A. puberula*
Leaves, stems and pedicels variously pubescent but seldom if ever all of them hairy at once 19

19(18). Stems usually numerous, less than 2 dm tall; flowers bright pink to lavender or purple; plants of high elevations in Wasatch and Uinta mountains .... *A. lemmonii*
Stems usually solitary or, if more, over 3 dm tall; flowers pale pink to lavender or white; plants of lower to moderate elevations, not of alpine sites 20

20(19). Petals 8-12 mm long or more; pedicels and siliques merely spreading; plants evidently rare in northern Utah .... *A. sparsiflora*
Petals 4-9 mm long; pedicels and siliques spreading-descending to reflexed 21

21(20). Basal leaves thickish, usually entire; pedicels merely spreading-descending .... *A. lignifera*
Basal leaves thin, often sharply toothed; pedicels curved-decending to reflexed; our most common species .... *A. holboellii*

Arabis confinis S. Wats. [*Turritis brachycarpa* Torr. & Gray; *A. drummondii* var. *brachycarpa* (Torr. & Gray) A. Gray; *A. confinis* var. *brachycarpa* (Torr. & Gray) Wats. & Coult.; *A. divaricarpa* A. Nels.; *A. brachycarpa* (Torr. & Gray) Britton, not Rupr.; *A. oblanceolata* Rydb.; *A. pratincola* Greene; *A. nemophila* Greene; *A. dacotica* Greene; *A. brevisiliqua* Rydb.; *A. stokesiae* Rydb.; *A. drummondii* var. *pratincola* (Greene) Hopkins]. Plants biennial or short-lived perennial; stems (2.5) 3-9 (10) dm tall, solitary, or, when more than one, not arising from between basal rosette and a tuft of ascending leaves; herbage subglabrous to puberulent with malpighian or 3- to several-rayed hairs at least on lower stems and leaves; basal leaves (1.3) 2-7 cm long, 0.3-0.9 cm wide, oblanceolate, subentire to dentate, usually acute; cauline leaves auriculate, numerous, mostly 2.2-6.5 cm long and 0.3-0.8 cm wide; pedicels 3-14 mm long, glabrous, spreading-ascending or even (rarely) descending; sepals 3-5 mm long, sparsely pubescent or glabrous; petals 6-10 mm long, pink to lavender, spatulate, erect or ascending; siliques 20-85 mm long, 1.5-2.5 mm wide, divaricate to subpendulous, valves glabrous, nerved to the middle or above; styles short or obsolete; seeds uni- or biseriate.— Moist sites at middle elevations in the mountains of Cache, Carbon, Garfield, Millard, Rich, Salt Lake, Sevier, Summit, Utah, Washington, Wayne, and Weber counties, and to be sought elsewhere; Alaska and southern Yukon east to the Atlantic and south to California and Colorado. Our material is var. *confinis*.

We are reluctantly taking up the name *Arabis confinis* for one of North America's more common species of the genus and placing the long-used name, *A. divaricarpa* A. Nels., in synonymy. The nomenclatural problems surrounding *A. confinis* were initially discussed by Fernald (Rhodora 5: 225-231. 1903) and reviewed again by Hopkins (Rhodora 39: 63-98, 106-148, 155-186. 1937) and Rollins (1941). Fernald correctly noted that Watson based his description on, and cited representative specimens of, two different kinds of *Arabi*, one being *A. drummondii* A. Gray, and the second *A. brachycarpa* (Torr. & Gray) Britton. What Fernald did not realize, apparently, was that the name *A. brachycarpa* had already been used by Ruprecht in an 1869 publication. Thus, Hopkins and Rollins took up the next available species name, *A. divaricarpa*, which was published by Nelson in 1900. Neither Hopkins nor Rollins attempted to typify the Watson name on one or the other of these elements (*A. drummondii* or *A. divaricarpa*) and simply placed *A. confinis* in synonymy under both.

We have reviewed the original Watson publication (Proc. Amer. Acad. Arts 22: 466. 1887) and have noted that under the current International Code, it is clear that Watson was proposing a new name for *Turritis brachycarpa* Torr. & Gray (not *Arabis brachycarpa* Rupr.), and, in spite of Watson's confused description and citation of specimens, one must accept *A. confinis* as a new name for *T. brachycarpa* and its type. Thus, *A. confinis* is the earliest available name for *T. brachycarpa*, and it is not a synonym of *A. drummondii* as proposed by Fernald, Hopkins, and Rollins.

In addition to var. *confinis*, there is also *Arabis confinis* var. *interposita* (Greene) Welsh and Reveal, comb. nov., based on *A. interposita* Greene, Leafl. Bot. Observ. 2: 78. 1910.

Arabis demissa Greene. [*A. rugocarpa* Osterh. *A. aprica* Osterh. ex Nels. in Coult. and Nels.] Plants perennial, stems 1-3 dm tall, solitary or 2-5 from a simple caudex, these arising from between the basal rosette and a tuft of ascending leaves, subglabrous to hirsute with simple or forked hairs at least below; basal leaves 1.5-3.5 cm long, 0.2-0.5 cm wide, narrowly to broadly oblanceolate, entire, hirsute marginally and often on surface with simple hairs; cauline leaves sessile and non-auriculate (except in var. *lanugida*), mostly 0.5-1 cm long and 0.1-0.4 cm wide, oblong to lanceolate, hirsute to glabrous; pedicels 3-7 mm long, glabrous, slender, arched downward; sepals 2-3.5 mm long, sparsely pubescent; petals 4.5-6.5 mm long, white to pink, spatulate, erect or ascending; siliques 20-40 mm long, 1.5-2 mm wide, pendulous, valves glabrous, nerved to about the middle; styles obsolete; seeds uniseriate.— Foothills and drainages in the Wasatch Plateau and eastern portion of the Uinta Mountains, Utah; southern Wyoming and central Colorado.

The species is closely allied to both *A. fendleri* and *A. pendulina*, differing from the former in smaller size of stems and leaves, from the latter in the more slender siliques, and from both of them in the uniseriate seeds.

1. Cauline leaves auriculate; basal leaves, at least the outer ones, oblanceolate .... var. *lanugida*
   Cauline leaves merely sessile, not auriculate; basal leaves merely linear to narrowly oblanceolate .... var. *russeola*

Var. *lanugida* Rollins. Low hills and drainages, sagebrush and juniper communities, at about 1500 to 1700 m elevation, Daggett and Emery counties; southern Wyoming.

Var. *russeola* Rollins. Low hills and valleys in juniper communities, at about 1700 m elevation, Daggett and Uintah counties; southern Wyoming.

These two variants are only weakly distinguishable and may not deserve separation. The var. *demissa* is restricted to the mountains of central Colorado.

Arabis drummondii A. Gray. [*Turritis stricta* Graham, not *A. stricta* Huds.; *Streptanthus angustifolius* Nutt. ex Torr. & Gray, not *A. angustifolia* Lam.; *A. connexa* Greene; *A. oxyphylla* Greene; *A. albertina* Greene; *A. philonipha* A. Nels. ex Rydb.; *Turritis drummondii* (A. Gray) Lunell; *A. drummondii* var. *connexa* (Greene) Fern.; *A. drummondii* var. *oxyphylla* (Greene) Hopkins]. Plants biennial or short-lived perennial, the stems (0.8) 1.2-9 (9.7) dm tall, solitary or 2 to several from a simple or branched caudex, not arising from between basal rosette and tuft of ascending leaves, usually glabrous throughout or strigose with malpighian hairs at base only; basal leaves (1.1) 1.5-7 (8) cm long, 0.2-1.2 cm wide, oblanceolate, entire, subglabrous or pubescent with malpighian hairs; cauline leaves usually longer than internodes, numerous, (1) 1.5-6 cm long, 0.2-1.5 cm wide, oblong to lanceolate, usually entire, sessile and auriculate, usually glabrous; pedicels 7-15 mm long in fruit, erect, glabrous; sepals (3) 3.3-5.7 mm long, glabrous; petals 6.5-10.5 mm long, white to pink, spatulate, ascending to erect; siliques (27) 35-95 (110) mm long, (1.2) 1.5-2 (3) mm wide, erect, valves glabrous, nerved to middle or above; styles short or obsolete; seeds biseriate.— Woodlands and meadows at moderate to high elevations, in Beaver, Cache, Duchesne, Garfield, Grand, Iron, Juab, Kane, Millard, Piute, Rich, Salt Lake, San Juan, Sanpete, Sevier, Summit, Uintah, Wasatch, Washington, Wayne, and Weber counties; Alaska and Yukon east to the Atlantic and south to California, Arizona, and New Mexico.

Arabis fendleri (S. Wats.) Greene. Plants perennial or rarely biennial, stems (1.4) 2-6 dm tall, solitary or 2-5 or more from a simple, or rarely branched, caudex, not arising from between the basal rosette and a tuft of ascending leaves, variously hairy to subglabrous with coarse simple or branched hairs at base only; basal leaves (1) 1.5-6 cm long, (0.2) 0.3-1.3 (1.5) cm wide, oblanceolate, coarsely dentate to subentire, ciliate with simple or forked hairs, surfaces similarly hairy to subglabrous; cauline leaves usually longer than internodes, several to numerous, (0.5) 1-3.5 (4) cm long, 0.3-0.7 cm wide, oblong to lanceolate, entire or rarely toothed, sessile and auriculate, glabrous or lower ones hairy; pedicels 4-18 mm long in fruit, ascending-spreading to descending, glabrous; sepals 2.3-5 mm long, pubescent or glabrous, more or less gibbous; petals 5-7 (8) mm long, white to pink, spatulate, ascending to erect; siliques 30-46 (60) mm long, 1.5-2.1 (2.5) mm wide, divaricate to curved pendulous, valves glabrous, nerved to middle or above; styles obsolete; seeds biseriate.— Woodlands, shrublands, and grasslands from low to moderate elevations, in eastern and southern Utah; Wyoming and Colorado west to Nevada, and south to Texas and Mexico.

1. Basal leaves dentate, definitely oblanceolate; petals usually pink .... *A. fendleri* var. *fendleri*
   Basal leaves entire, narrowly oblanceolate; petals white ...... *A. fendleri* var. *spatifolia*

Var. ***fendleri.*** [*A. holboellii* var. *fendleri* S. Wats. in Gray] Garfield, Millard, Piute, San Juan, Sevier, and Washington counties; range of the species.

Var. ***spatifolia*** (Rydb.) Rollins. [*A. spatifolia* Rydb.] Known only from Daggett County; Wyoming, Colorado, and New Mexico.

Arabis glabra (L.) Bernh. Plants biennial or rarely perennial, stems 3-8 (10) dm tall, solitary or 2 or 3, from a taproot, not arising from between the basal rosette and a tuft of ascending leaves, usually hirsute with simple or forked hairs, rarely with appressed dendritic hairs, at base only; basal leaves 3-10 (15) cm long, 0.8-3.5 (5) cm wide, oblong-oblanceolate to spatulate, sinuate-dentate to entire, more or less ciliate with forked or dendritic hairs, surfaces (especially the veins) hirsute with simple or forked hairs; cauline leaves usually longer than internodes (at least below), numerous, 1.5-9 (12) cm long, 0.4-2.3 (3.5) cm wide, lanceolate, denticulate to entire, sessile and auriculate, glabrous at least above; pedicels 4-12 mm long in fruit, erect, often appressed, glabrous; sepals 3.3-4.5 mm long, glabrous, often tinged reddish-purple; petals 4.7-6 (7) mm long, cream or rarely pinkish, narrowly spatulate, ascending to erect; siliques 40-90 mm long, 1-1.5 mm wide, strictly erect, valves glabrous, nerved to the middle or above; styles about 0.5 mm long, stigma 0.8-1.1 mm broad; seeds more or less biseriate.— Sagebrush, oak, and woodland communities at low to moderate elevations in northern Utah; widespread in North America; Europe.

1. Pubescence of stem base appressed, of several-branched hairs .... *A. glabra* var. *furcatipilis*
   Pubescence of stem base hirsute with simple or merely forked hairs .... *A. glabra* var. *glabra*

Var. ***furcatipilis*** Hopkins. Cache and Salt Lake counties, and to be expected elsewhere; Utah and California.

Var. ***glabra.*** [*Turritis glabra* L.; *A. perfoliata* Lam.; *T. macrocarpa* Nutt. ex Torr. and Gray; *A. macrocarpa* (Nutt.) Torr.] Box Elder, Millard, Tooele, Uintah, Utah, Wasatch, and Weber counties; range of the species.

Arabis hirsuta (L.) Scop. [*Turritis hirsuta* L.] Plants biennial or perennial, stems (0.9) 1.5-6 (7) dm tall, solitary or more commonly 2-6 or more, from a simple or branched caudex, not arising from between the basal rosette and a tuft of ascending leaves, hirsute with simple or forked hairs, at base at least; basal leaves (0.8) 1.5-6 (8) cm long, 0.3-1.8 (3) cm wide, elliptic to oblong or oblanceolate, entire or more or less dentate, ciliate with simple or forked hairs, surfaces glabrous or more or less hirsute with simple or forked hairs; cauline leaves usually longer than internodes at least below, numerous, (0.6) 1-5 cm long, 0.2-2 cm wide, oblong to lanceolate, toothed to entire, sessile and auriculate, rarely merely sessile, hirsute or glabrous; pedicels 3-18 mm long in fruit, erect, appressed, glabrous; sepals 2.2-4 (4.5) mm long, glabrous or sparingly hairy, seldom tinged reddish-purple; petals 3.2-7 (9) mm long, white or pink, oblong to spatulate, ascending to erect; siliques 30-55 (60) mm long, 1-1.5 (2) mm wide, valves glabrous, erect, nerved to above the middle; styles 0.3-1 mm long, stigma 0.3-0.7 mm broad; seeds uniseriate.— Moist woods at moderate to high elevations; Alaska and Yukon east to the Atlantic and south to California, Arizona, and New Mexico; circumboreal.

1. Flowers 5-9 mm long; siliques often more or less divergent .... *A. hirsuta* var. *glabrata*
   Flowers 3-5 mm long; siliques strictly erect .... *A. hirsuta* var. *pycnocarpa*

Var. ***glabrata*** Torr. & Gray. [*Turritis spathulata* Nutt. ex Torr. & Gray; *A. rupestris* Nutt. ex Torr. & Gray; *A. pycnocarpa* var. *glabra* (Torr. & Gray) Hopkins].

Raft River Mts., Box Elder Co. (US), and Deep Creek Mts., Juab Co., Utah; British Columbia south to California, east to Wyoming and Utah.

Var. *pycnocarpa* (Hopkins) Rollins. [*Turritis ovata* Pursh?; *A. hirsuta* var. *ovata* (Pursh) Torr. & Gray?; *A. pycnocarpa* Hopkins] Mountains in northern and central Utah; Daggett (US), Duchesne, Emery, Garfield, Kane, Piute, Salt Lake, Sevier (US), Uintah (US), Utah, and Wasatch counties; widespread in North America.

The name "*ovata*" may have priority over the name "*pycnocarpa*", but, until the type of the Pursh name can be discovered, the description is inadequate to know exactly which species of *Arabis* Pursh had in mind, and thus the name cannot be applied to our plants.

Arabis holboellii Hornem. Plants biennial or perennial, stems (1) 2-11.5 dm tall, solitary or less commonly 2-6, from a simple or branching caudex, not arising from between the basal rosette and a tuft of ascending leaves, pubescent with appressed or spreading hairs, at least at base; basal leaves (1) 1.5-5.5 cm long, 0.2-8 mm wide, elliptic to oblanceolate, entire to dentate, with dendritic hairs on margins and usually on surfaces, rarely with some simple or forked hairs near petiole base; cauline leaves usually longer than internodes, at least below; numerous, 1.2-6.5 cm long, 0.2-0.9 cm wide, oblong to lanceolate, entire or some toothed, sessile and auriculate, pubescent to glabrous; pedicels 5-23 mm long in fruit, reflexed to loosely descending, glabrous or pubescent; sepals 2.9-5 mm long, pubescent or glabrous, often tinged reddish; petals 4-9 (10) mm long, pink to lavender or white, spatulate, erect or ascending; siliques (20) 25-70 mm long, 1-2.5 mm wide, reflexed to loosely pendulous, the valves glabrous, nerved to below or above middle; style obsolete or very short, stigma not much enlarged; seeds biseriate.— Foothills and mountains from lower to moderate elevations among shrubs or in woods; Alaska and Yukon east to Greenland and south to California, Utah, Colorado, and Nebraska.

1. Pedicels gently curved downward; pods pendulous, often somewhat curved inward .... *A. holboellii* var. *pinetorum*
   Pedicels abruptly curved at the base, deflexed; siliques strictly reflexed to descending and often straight .... *A. holboellii* var. *secunda*

Var. *pinetorum* (Tidestr.) Rollins. [*A. pinetorum* Tidestr.] Widespread in Beaver, Box Elder, Cache, Daggett, Duchesne, Emery, Garfield, Juab, Kane, Millard, Salt Lake, Sevier, Summit, Uintah, Utah, Wasatch, and Washington counties; Saskatchewan to British Columbia south to California, Colorado, and Nebraska.

Var. *secunda* (Howell) Jeps. [*A. retrofracta* Grah.; *Turritis retrofracta* (Grah.) Hook.; *Streptanthus virgatus* Nutt. ex Torr. and Gray; *A. secunda* Howell; *A. arcuata* var. *secunda* (Howell) Robins.; *A. holboellii* var. *retrofracta* (Grah.) Rydb.; *A. rhodantha* Greene; *A. exilis* A. Nels.; *A. tenuis* Greene; *A. lignipes* A. Nels.; *A. consanguinea* Greene; *A. kochii* Blankinship, not Jordan; *A. sparsiflora* var. *secunda* (Howell) Piper; *A. caduca* Greene; *A. macdougalii* Rydb.] Widespread and common in Beaver, Cache, Daggett, Davis, Duchesne, Grand, Millard, Piute, Salt Lake, San Juan, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, and Weber counties; Quebec to Alaska and British Columbia, south to California and Colorado.

The name var. *secunda* is taken up for our most common species of the genus as the varietal rank was first occupied by "*secunda*" (1895), one year ahead of Rydberg's publication of var. *retrofracta*.

Arabis lemmonii S. Wats. [*A. canescens* var. *latifolia* S. Wats.; *A. latifolia* (S. Wats.) Piper; *A. bracteolata* Greene; *A. egglestonii* Rydb.] Plants perennial, the stems 0.5-2 dm tall, several to many from a branching caudex, often with tufts of ascending leaves, pubescent to glabrous; basal leaves 0.8-2 (2.5) cm long, 0.2-0.5 cm wide, spatulate to oblanceolate, usually entire, marginally pubescent with dendritic hairs, rarely with some hairs simple or forked on the petiole bases, surfaces densely pubescent with dendritic hairs; cauline leaves shorter or longer than internodes, few, 0.4-1.5 cm long, 0.1-0.3 cm wide, elliptic-oblong to lanceolate, entire, sessile and auriculate (at least some), pubescent to glabrous; pedicels 2-6 mm long in fruit, ascending to spreading, glabrous or pubescent; sepals 2-3.5 mm long, glabrous or pubescent, often purplish; petals 4-5.5 (6) mm long, pink to lavender, spatulate, erect to ascending; siliques mostly 20-50 mm long, (1.5) 2-2.5 (3) mm wide, ascending, spreading or somewhat pendulous, valves glabrous, nerved to middle; seeds uniseriate.— Mountain summits at high elevations, mostly 3300-4000 m elevation, in Duchesne, Summit, and Salt Lake counties; Alaska and Yukon south to California, Colorado, and Montana.

Our plant is var. *lemmonii.*

Arabis lignifera A. Nels. Plants perennial, the stems 1.5-6 dm tall, solitary or 2-5 from a simple or branching caudex, not arising from between basal rosette and a tuft of ascending leaves, more or less densely pubescent with dendritic hairs, at least below; basal leaves 1.5-4 (5) cm long, 0.3-1 cm wide, spatulate to oblanceolate, entire or nearly so, densely pubescent with dendritic hairs, rarely with long simple or forked hairs on the petiole base; cauline leaves from longer to shorter than internodes, numerous, 0.8-3.5 cm long, 0.2-1 cm wide, oblong to lanceolate, sessile and auriculate, pubescent to glabrous; pedicels (3) 5-15 mm long in fruit, spreading to arching downward, glabrous or pubescent; sepals 3-5.6 mm long, pubescent or glabrate; petals 5.2-9.1 mm long, pink to lavender, spatulate, erect or ascending; siliques 30-60 (65) mm long, 1.5-2 mm wide, more or less spreading-pendulous, the valves glabrous, nerved to middle or above; style short or obsolete, stigma not or only slightly expanded; seeds uniseriate to more or less biseriate.— Foothills and desert ranges at moderately low to low elevations in desert shrub, sagebrush, and juniper-pinyon woodlands in Beaver, Box Elder, Carbon, Daggett, Duchesne, Iron, Juab, Kane, Millard, Salt Lake, San Juan, Summit, Tooele, and Uintah counties; Wyoming and Idaho south to Nevada and Arizona.

Arabis lyallii S. Wats. [*A. drummondii* var. *alpina* S. Wats.; *A. oreophila* Rydb.; *A. armerifolia* Greene; *A. densa* Greene; *A. multiceps* Greene; *A. drummondii* var. *lyallii* (S. Wats.) Jeps.; *A. drummondii* var. *oreophila* (Rydb.) Hopkins]. Plants perennial, stems 0.3-2.5 dm tall, few to many from a branching caudex, often with tufts of ascending leaves, glabrous; basal leaves 0.5-2.5 cm long, 0.2-0.6 cm wide, oblanceolate to spatulate, entire, glabrous or margin and surfaces sparingly pubescent with dendritic hairs; cauline leaves shorter to longer than internodes, few, 0.6-2 cm long, 0.2-0.6 cm wide, ovate to lanceolate or oblong, entire, sessile and at least some auriculate, usually glabrous; pedicels 4-10 (13) mm long, erect-ascending, glabrous; sepals 3.3-4.5 mm long, glabrous, not or only slightly gibbous, often purplish; petals 7-9 (10) mm long, bright pink to lavender, spatulate, erect or ascending; silique 20-60 mm long, 2-3 mm wide, erect-ascending, valves glabrous, nerved to middle; style short, stigma not or slightly enlarged; seeds uniseriate or more or less biseriate.— Alpine tundra, krumholz, glacial moraines and among subalpine conifers, at 2600-3700 m elevation in Cache, Daggett, Duchesne, Millard, Salt Lake, Uintah, Utah, Wasatch, and Weber counties; Yukon and British Columbia south to California, Nevada, northern Utah, and western Wyoming. Our material is var. *lyallii.*

Arabis microphylla Nutt. ex Torr. & Gray. Plants perennial, stems 0.5-3 (5) dm tall, several to many from a branching caudex, tufts of ascending leaves lacking or poorly developed, glabrous throughout or hairy below with simple or forked hairs; basal leaves 0.7-2.5 cm long, 0.2-0.5 cm wide, oblanceolate to spatulate, entire or rarely toothed, margins with dendritic or merely sessile and forked hairs, densely pubescent with minute dendritic hairs; cauline leaves often shorter than internodes, few, 0.6-2 cm long, 0.1-0.6 cm wide, oblong to lance-linear, entire or some toothed, sessile and auriculate, glabrous or lowermost pubescent; pedicels 4-13 (15) mm long, ascending to spreading-ascending, glabrous or pubescent; sepals 2.5-4 mm long, glabrous or pubescent, often purplish; petals 5-8 mm long, pink to lavender, spatulate, ascending to erect; siliques (20) 25-60 mm long, 1.2-2 mm wide, erect to spreading, nerved at base only; style developed or obsolete, stigma not expanded; seeds uniseriate.— Foothills and mountains at moderate elevations; British Columbia to Montana, south to Oregon, Nevada, and western Wyoming.

1. Stems mostly 2.5-5 dm tall; pedicels and siliques spreading .... *A. microphylla* var. *macounii*
   Stems mostly less than 2 dm tall; pedicels divaricate, the siliques erect .... *A. microphylla* var. *microphylla*

Var. *macounii* (S. Wats.) Rollins. [*A. macounii* S. Wats.; *A. densicaulis* A. Nels.] Mill Creek Canyon, Salt Lake County, and Uintah County, and to be expected elsewhere; Montana to British Columbia, south Idaho, Wyoming, and Utah.

Var. *microphylla*. [*A. tenuicola* Greene] Low to moderate elevations, often on rock outcrops or talus, Cache, Grand (?), Salt Lake, Utah and Weber counties; Montana to Washington, south to Nevada, Utah, and Wyoming.

Arabis nuttallii Robinson in Gray. [*A. spathulata* Nutt. ex Torr. & Gray, not DC.; *Erysimum nuttallii* (Robinson) Kuntze; *A. bridgeri* M. E. Jones; *A. macella* Piper] Plants perennial, stems 0.9-3 dm tall, several to many from a branching caudex, tufts of ascending leaves lacking, glabrous throughout or hirsute below with simple or forked hairs; basal leaves 1-4 cm long, 0.4-1.2 cm wide, oblanceolate, usually entire, ciliate and hairy on lower surface (at least) with long simple and often with some forked hairs; cauline leaves shorter than internodes, few, 0.5-2 cm long, 0.1-0.7 cm wide, elliptic to oblong, lanceolate or oblanceolate, entire, sessile or subsessile, not auriculate, hairy or the upper glabrous; pedicels 5-20 mm long, spreading-ascending, glabrous; sepals 3-4 mm long, glabrous or sparingly hirsute, usually green or cream; petals (5) 6-8 mm long, white or lavender, spatulate, more or less spreading; siliques (8) 12-20 mm long, 1-1.5 mm wide, erect to spreading, valves glabrous, nerveless or faintly nerved; style about 1 mm long, stigma not especially expanded; seeds uniseriate.— Meadows and shrublands from low elevations to mountain summits in Cache and Wasatch counties, and to be expected elsewhere; Alberta south to Wyoming and northern Utah.

Arabis pendulina Greene. [*A. setulosa* Greene; *A. diehlii* M. E. Jones; *A. nevadensis* Tidestr.] Plants perennial, the stems 0.6-3.5 (4) dm tall, (one) several to many from a simple or branched caudex, arising from between basal rosette and a usually well-developed tuft of ascending leaves, hirsute with simple hairs below or glabrous throughout; basal leaves 0.8-4 cm long, 0.1-1 cm wide, spatulate to narrowly oblanceolate, entire, ciliate and hairy on one or both surfaces with long simple hairs or totally glabrous; cauline leaves much shorter than internodes, few, 0.3-1.2 cm long, 0.1-0.6 cm broad, oblong to lanceolate, entire, sessile and usually not auriculate (but sometimes slightly clasping), hairy or the upper glabrous; pedicels 3-6 (10) mm long, arched downward, glabrous; sepals 2.5-3.6 (4) mm long, usually purplish; petals 4.8-6.8 mm long, pink to lavender, spatulate, erect or ascending; siliques (10) 13-40 mm long, 1.6-2.3 (3) mm wide, pendulous, valves glabrous, nerved below middle; style obsolete or very short, stigma not enlarged; seeds biseriate.— Open knolls to forest ground layer, from 1670 to 3400 m elevation, in pinyon-juniper, ponderosa pine, and spruce-fir communities in Emery, Garfield, Kane, Piute, Sevier, Wayne, and Washington counties; eastern and southern Nevada east to Utah.

Plants from some sites have clasping leaves but otherwise seem not to differ in any other way from the more typical specimens with non-auriculate leaves.

Arabis perennans S. Wats. [*A. arcuata* var. *perennans* (S. Wats.) M. E. Jones; *A. gracilenta* Greene; *A. eremophila* Greene; *A.*

recondita Greene; *A. angulata* Greene ex Woot. & Standl.] Plants perennial, stems 0.9-5.5 (6) dm tall, (one) several to many from simple or branching herbaceous to woody caudex, arising from between basal rosette and a tuft of ascending leaves, pubescent with dendritic hairs on margin and on surfaces, rarely with simple or forked hairs along petiole base; cauline leaves longer than internodes at least below, several, 0.7-4 cm long, 0.2-0.8 cm wide, oblong to lanceolate, entire to toothed, hairy or the upper glabrous; pedicels 4-24 mm long, spreading to arched downward, glabrous or pubescent; sepals 3-4 (4.5) mm long, often purplish, usually dendritic hairy; petals 5-7 (9) mm long, pink to lavender, spatulate, erect or spreading; siliques (20) 27-55 (60) mm long, 1.2-2 mm wide, spreading to pendulous, valves glabrous, nerveless or nerved at the base; style obsolete or very short, stigma not enlarged; seeds uniseriate.— Warm desert shrub, pinyon-juniper, sagebrush, ponderosa pine, and oakbrush communities at low to moderate elevations in Beaver, Carbon, Emery, Garfield, Grand, Kane, Millard, Piute, San Juan, Sanpete, Sevier, Wayne, and Washington counties; Colorado and New Mexico to Nevada, California, and Baja California.

Our specimens are far from uniform, with some approaching *A. lignifera* on the one extreme, and *A. selbyi* on the other.

Arabis puberula Nutt. ex Torr. & Gray. [*A. beckwithii* S. Wats.; *Erysimum puberulum* (Nutt.) Kuntze; *A. subpinnatifida* var. *beckwithii* (S. Wats.) Jeps.; *A. arida* Greene; *A. lignipes* var. *impar* A. Nels.; *A. sabulosa* M. E. Jones; *A. sabulosa* var. *frigida* M. E. Jones; *A. sabulosa* var. *colorata* M. E. Jones; *A. subpinnatifida* var. *impar* (A. Nels.) Rollins] Plants perennial or infrequently biennial, stems (0.7) 1-3 dm tall or more, solitary or few from a simple caudex, not arising from between a basal rosette and a tuft of ascending leaves, pubescent throughout with dendritic hairs, rarely glabrous above; basal leaves 1-2.5 (3) cm long, 0.2-0.6 cm wide, oblanceolate, entire or toothed, pubescent with minute dendritic hairs; cauline leaves usually longer than internodes, several to many, 1-3 cm long, 0.2-0.8 cm wide, toothed to entire, sessile and at least some auriculate, hairy like the basal leaves; pedicels 2-7 mm long, arched downward, pubescent; sepals 3.5-6 mm long, dendritic hairy; petals 7-11 mm long, pink to white, spatulate, erect or ascending; siliques (25) 30-50 (60) mm long, 2-3 mm wide, pendulous to reflexed, valves copiously hairy to glabrate, nerved to below middle; style obsolete, stigma not enlarged; seeds uniseriate.— Oakbrush community at moderate elevations in Salt Lake County (*Rose 1048*, BRY), and to be sought elsewhere; Washington and Idaho south to California and Nevada.

A closely related species, *Arabis cobrensis* M. E. Jones, is to be sought in extreme northern Utah. The species occurs just north of the state line in Uinta County, Wyoming, and in northeastern Elko County, Nevada, but as yet it is not known from Utah. *Arabis cobrensis* is a well-defined perennial with a well-branched caudex, the basal leaves are only 0.1-0.3 cm wide, the few cauline leaves are remote and only 0.1-0.3 cm wide, and the petals are 4-6 mm long. It is to be sought in Daggett and Box Elder counties.

Arabis pulchra M. E. Jones. Plants perennial, stems 1.5-6 dm tall, solitary or several from a branching herbaceous to woody caudex, not arising from between basal rosette and a tuft of ascending leaves, pubescent with dendritic hairs throughout or glabrous above; basal leaves in poorly developed rosettes, 1-6 cm long, 0.2-0.6 cm wide, narrowly oblanceolate to spatulate, entire, densely hairy with minute hairs; cauline leaves shorter or longer than internodes, many, 1.2-6 cm long, 0.1-0.5 cm wide, entire, sessile and mostly not auriculate, hairy like the basal leaves; pedicels 5-18 mm long, recurved to pendulous in fruit, pubescent to glabrate; sepals 5-8.2 mm long, more or less gibbous, dendritic-pubescent, often purplish; petals 9-18.5 mm long, pale pink to white or pink to lavender or purple, spatulate to obovate-spatulate, spreading or ascending to erect; siliques 35-55 (65) mm long, 1.8-2.5 (3) mm wide, pendulous to reflexed, valves copiously hairy to glabrate, nerved to middle or above; style obsolete or very short, stigma not expanded; seeds biseriate.— Desert shrub, pinyon-juniper, and sagebrush communities from 650 to 2000 m elevation in the southern two-thirds of Utah; common from Colorado and New Mexico west to California and Baja California.

1. Flowers lavender to purple, 9-11 mm long; petals ascending to erect .... *A. pulchra* var. *munciensis*
   Flowers pale pink or white, less commonly lavender, 10-18.5 mm long; petals spreading .... *A. pulchra* var. *pallens*

Var. *munciensis* M. E. Jones. Desert shrublands in Beaver, Juab, Iron, Kane, Millard, Tooele, and Washington counties; Nevada and California.

Var. *pallens* M. E. Jones. [*A. formosa* Greene] Desert shrublands to pinyon-juniper zone in Duchesne, Emery, Garfield, Grand, Kane, San Juan, Uintah and Wayne counties; Colorado, New Mexico, and Arizona.

Arabis selbyi Rydb. Plants perennial, the stems 1.5-4 (5) dm tall, usually several from a simple or branching caudex, arising from between basal rosette and an ascending tuft of leaves, pubescent below with dendritic or forked hairs; basal leaves 1.5-4 (6) cm long, 0.2-1 cm wide, oblanceolate to spatulate, usually entire, densely to sparsely pubescent with dendritic hairs on margin and surfaces, sometimes with simple or branched hairs along petiole base; cauline leaves usually shorter than internodes, few to several, 0.3-2.5 (3) cm long, 0.1-0.4 cm wide, narrowly oblong to lanceolate, entire, hairy or glabrous; pedicels 4-15 mm long in fruit, spreading-ascending, glabrous or pubescent; sepals 2.6-3.5 (4) mm long, often purplish, usually dendritic hairy; petals 5-7 (8) mm long, pink to lavender, spatulate, erect or ascending; siliques 30-55 (60) mm long, 1.2-1.8 mm wide, spreading-ascending to more or less pendulous, valves glabrous, nerved at base or nerveless; style obsolete or very short, stigma not enlarged; seeds uniseriate.— Sagebrush and pinyon-juniper communities mostly between 1500 and 2200 m elevation in Carbon, Duchesne, Emery, Garfield, Grand, San Juan, Uintah, and Utah counties; western Colorado and northwestern New Mexico.

Only the slightly more ascending pedicels and usually entire or subentire leaves serve to distinguish this entity from *Arabis perennans*. Possibly, it would be treated better at an infraspecific level within that species.

Arabis shockleyi Munz. Plants perennial or infrequently biennial, stems 1.2-3.5 (4) dm tall, solitary or 2-4 from a simple or branching caudex, not arising from between a basal rosette and a tuft of ascending leaves, densely pubescent throughout with minute dendritic hairs, often somewhat less densely so above; basal leaves 1.6-3 (3.5) cm long, 0.5-0.9 cm wide, oblanceolate to spatulate, entire, densely pubescent throughout with dendritic hairs only; cauline leaves much longer than internodes, numerous, 1.2-3 cm long, 0.5-1.2 cm wide, ovate-lanceolate to lance-attenuate, entire or nearly so, sessile and auriculate, hairy as on basal leaves; pedicels 12-17 mm long in fruit, ascending, pubescent; sepals 5.5-7 mm long, often reddish, dendritic hairy; petals 7.5-10 mm long, pink to lavender, spatulate, erect or ascending; siliques 42-65 mm long, 1.2-1.8 mm wide, ascending to spreading, valves glabrous, nerved to about middle; style up to 0.8 mm long, stigma not much expanded; seeds biseriate.— Desert shrublands and pinyon-juniper communities mostly 1430 to 1900 m elevation in Juab, Millard, and Tooele counties; north-central and western Nevada, and in eastern and southern California.

Arabis sparsiflora Nutt. ex Torr. and Gray. Plants perennial, stems 2.3-10 dm tall, solitary or less commonly 2 or more from a simple or branching caudex, not arising from between the basal rosette and a tuft of ascending leaves, pubescent with appressed or spreading hairs at least below; basal leaves 3-7 (9) cm long, 0.3-0.6 (0.9) cm wide, oblanceolate, entire or dentate, pubescent with coarse dendritic hairs usually on both surfaces; cauline leaves longer than internodes, numerous, 1.5-6 cm long or more, 0.3-0.7 cm wide, oblong to lanceolate, entire or the lower toothed, sessile and auriculate, hairy like the basal leaves or wholly glabrous; pedicels 5-15 mm long, ascending-spreading, glabrous or pubescent; sepals 4.7-6 mm long, dendritic hairy; petals 8-12 mm long, pink to lavender or purple, spatulate, ascending to erect; siliques 60-100 (120) mm long, 1.2-2 mm wide, ascending to curved-descending; style obsolete or nearly so, stigma not expanded; seeds uniseriate.— Foothills and canyons at low to moderate elevations in oakbrush, sagebrush, and streamside forest communities of northern Utah; British Columbia and Alberta south to California, Utah, and Wyoming.

1. Basal leaves entire, narrowly oblanceolate; pedicels ascending-spreading .... *A. sparsiflora* var. *sparsiflora*
   Basal leaves dentate, oblanceolate; pedicels spreading ..... *A. sparsiflora* var. *subvillosa*

Var. *sparsiflora*. [*A. peramoena* Greene; *A. sparsiflora* var. *peramoena* (Greene) Rollins] Foothills and stream courses in Cache, Salt Lake, and Weber counties; California, Oregon, and Idaho.

Var. *subvillosa* (S. Wats.) Rollins. [*A. arcuata* var. *subvillosa* S. Wats.; *A. perelegans* Nels. in Coult. and Nels.] Foothills and mountain slopes in Davis, Uintah, and Weber counties; Washington to Montana south to Wyoming, Utah, Nevada, and California.

ARMORACIA Gaertn.
Horse-Radish

Plants glabrous perennials from tuberous-thickened taproots; leaves alternate, simple, crenately toothed or lobed, petiolate to subsessile, not auriculate; flowers racemose, the pedicels ascending, not subtended by bracts; sepals 4, deciduous; petals 4, white, not emarginate; stamens 6, at least the 2 short stamens subtended by glands; style short, the capitate stigma hemispheric; fruit a silicle, bilocular, about as long as broad, obovoid-ellipsoid, the valves with an inconspicuous midnerve; seeds apparently never developing.

A genus of 3 species of Eurasia.

Armoracia rusticana Gaertn. [*Cochlearia armoracia* L.; *Nasturtium armoracia* (L.) Fries; *Rorippa armoracia* (L.) A. S. Hitchc.; *Radicula armoracia* (L.) A. Gray; *Armoracia armoracia* (L.) Cockerell] Plants perennial, stems 6-10 dm tall or more, few to many arising from summit of root crown; basal leaves oblong to oblong-lanceolate, blades 15-50 cm long, 10-15 cm wide, base cordate to rounded, petioles 0.6-4 dm long or more; cauline leaves reduced and only short petiolate to subsessile upwards, lanceolate to elliptic and crenately toothed to lobed, glabrous; pedicels mostly 8-11 mm long, ascending in fruit; sepals 2-2.5 mm long, caducous, greenish, glabrous; petals 4.2-4.5 (5) mm long, white, obovate-spatulate, surpassing sepals; silicles 3-6 mm long and about as wide, valves glabrous; styles 0.2-0.3 mm long, hemispheric stigma to 0.5 mm broad or more.— Cultivated and occasionally escaping and persistent as in Cache, Salt Lake, Summit, Utah, and Weber counties, and most likely elsewhere in agricultural regions of the state; widespread in North America; introduced from Eurasia.

ATHYSANUS Greene

Plants annuals with typically dendritic and with some simple hirsute hairs, arising from slender taproots; leaves alternate, simple, few-toothed, sessile, and not auriculate; flowers racemose, pedicels recurved, not subtended by bracts; sepals 4, deciduous; petals 4, white, not emarginate; stamens 6; style short, stigma capitate; fruit a silicle, unilocular, about as broad as long, orbicular, compressed, valves nerveless; seeds solitary.

A monotypic genus.

Athysanus pusillus (Hook.) Greene. [*Thysanocarpus pusillus* Hook.; *A. pusillus* var. *glabior* S. Wats.] Plants annual, stems erect or ascending, usually branched from near base, 0.8-3 dm tall; leaves ovate to obovate or spatulate (especially the lowermost), dendritic hairy on both surfaces; pedicels recurved, 1-4 mm long; sepals about 1 mm long, cream to purplish, glabrous; petals 1-2 mm long, white, oblong-spatulate, surpassing sepals; silicles 1.5-2.5 mm long and about as wide, valves hirsute with simple, uncinate hairs, emarginate at style; styles persistent, 0.2-0.3 mm long.— Dry sites at low elevations, not definitely known from Utah but to be expected in Washington County; British Columbia south to California and Arizona.

Barbarea R. Br.

Plants glabrous to sparsely hirsute biennials or rarely annuals from taproots; leaves alternate, lyrate-pinnatifid to pinnately compound, cauline leaves auriculate-clasping and often falsely petiolate above clasping base; flowers racemose, pedicels ascending to erect, not subtended by bracts; sepals 4, deciduous; petals 4, yellow, truncate to rounded apically; stamens 6, filaments lacking glandular processes; style stout, abruptly contracted to capitate stigma; fruit a silique, many times longer than broad, linear, only slightly compressed, more or less contracted between the seeds, valves 1-nerved; seeds numerous, uniseriate.

About 20 species of the northern temperate regions of the world.

Barbarea orthoceras Ledeb. [*B. americana* Rydb.; *Campe orthoceras* (Ledeb.) Heller; *B. orthoceras* var. *dolichocarpa* Fern.] Plants erect, stems 1.5-10 dm tall, glabrous; basal leaves lyrate-pinnatifid to pinnately compound, rarely reduced to terminal lobe, mostly (1.5) 4-15 (20) cm long, 1-2.5 (4) cm wide, glabrous or petiole and lower lobes sparsely hirsute; cauline leaves reduced upwards, auriculate-clasping; pedicels 2-4 mm long, glabrous, ascending; sepals 2.5-3.5 mm long, yellowish, glabrous; petals 4-5.5 mm long, yellow, spatulate-oblanceolate, ascending-spreading; siliques (15) 20-50 mm long, 1.5-2.5 mm wide, erect or ascending, valves glabrous, prominently nerved to apex; style beaklike, (0.5) 1-2 mm long, abruptly contracted to stigma; seeds uniseriate, pitted.— Moist meadows, roadsides, and openings in woods from 1350 to 2500 m elevation in Box Elder, Salt Lake, Utah, Wasatch, and Washington counties, and to be expected almost throughout the state; Alaska and Yukon east to the Atlantic and south to California, Nevada, Utah, and Colorado; Eurasia.

Berteroa DC.

Plants stellate-pubescent annuals or infrequently winter annuals from taproots; leaves alternate and basal, simple, entire, reduced upwardly and sessile, not auriculate; flowers racemose, pedicels erect-ascending, not subtended by bracts; sepals 4, deciduous; petals 4, white, deeply emarginate and often bilobed; stamens 6, the filaments lacking glandular processes; style long, slender, stigma capitate; fruit a silicle, 1-3 times longer than broad, compressed parallel to septum, valves 1-nerved or nerveless; seeds several.

About 8 species of worldwide distribution.

Berteroa incana (L.) DC. [*Alyssum incanum* L.] Plants erect, stems 3-10 dm tall or more, appressed stellate-hairy; basal leaves oblanceolate, 3-5 cm long, entire, petiolate, usually withered at anthesis; cauline leaves reduced upwards, sessile or short-petiolate below, stellate-hairy; pedicels erect or ascending, 4-10 mm long, stellate and sometimes more or less hirsute; sepals 2-3 mm long, greenish to whitish, stellate-hairy; petals 4-6 mm long, white, deeply bilobed; silicles 5-7 mm long, 2-3 mm wide, moderately inflated, stellate hairy; styles (1.5) 2-3 mm long, persistent.— Roadsides and other disturbed places, not definitely known from Utah but to be expected; widespread in North America; Europe.

Brassica L.

Plants glabrous or hirsute annuals from taproots; leaves alternate and basal, variously lobed to entire, basal ones often lyrate-pinnatifid, reduced upwardly and petiolate to sessile or auriculate; flowers racemose, pedicels erect or ascending, not subtended by bracts; sepals 4, deciduous; petals 4, yellow; stamens 6, filaments lacking glandular processes; styles slender to thick, mostly well developed, stigma capitate; fruit a silique, several to many times longer than broad, linear, terete or nearly so, often more or less constricted, valves 1—3-nerved, apical portion producing a stout 1—3-nerved beak; seeds several to many, uniseriate.

Several cultivated members of this genus are present in our region in addition to the weedy adventives distinguished below. They are: *Brassica caulorapa* Pasquale (kohlrabi); *B. napobrassica* Mill. (rutabaga); *B. oleracea* L. var. *botrytis* L. (cauliflower), var. *capitata* L. (cabbage), var. *gemifera* Zenker (brussel sprout), and var. *italica* Plenck (broccoli); and *B. rapa* L. (turnip).

1. Cauline leaves sessile, auriculate-clasping, glaucous and entire or nearly so .... *B. campestris*
   Cauline leaves petiolate and not auriculate, or, if rarely so, falsely petiolate above the clasping base 2

2(1). Valves of fruit, and often the pedicels and raceme rachis, hirsute with course, spreading hairs; plants cultivated and escaping .... *B. hirta*
   Valves of fruit, pedicels, and raceme rachis glabrous; plants adventive weeds 3

3(2). Silique with a flattened, 2-edged or angular beak, valves and beak strongly 3 (5)-nerved .... *B. kaber*
   Silique with a cylindrical or rarely slender-conic beak, valves and beak with 1 (rarely with 2 additional delicate) nerves 4

4(3). Pedicels 2-6 mm long; siliques 1-2.5 cm long, 1-1.8 mm wide, ascending-appressed .... *B. nigra*
   Pedicels mostly (5) 10-15 mm long; siliques 2-4 cm long, 2-3 mm wide, ascending to erect but not appressed .... *B. juncea*

Brassica campestris L. [*B. rapa* of authors, not L.; *B. napus* of authors, not L.] Plants erect, glabrous or with very few hairs, stems 2.5-10 dm long or more, simple or branched; basal leaves lyrate-pinnatifid, 5-18 cm long, terminal lobe mostly 2-5 cm wide, crenate-dentate; lower cauline leaves similar to basal ones, reduced upwards, becoming auriculate-clasping and dentate to entire; pedicels 7-20 mm long, slender, ascending, glabrous; sepals 4.5-6 mm long, yellowish to greenish; petals 6-10 mm long, yellow; siliques 30-70 mm long, (1.5) 2.5-3.5 mm thick, beak 8-15 mm long, 1-nerved, valves conspicuously 1-nerved and with 2 more or less delicate lateral nerves, glabrous.— Cultivated fields, roadsides, and waste places in Summit, Utah, and Washington counties, though probably cosmopolitan in the state; widespread in temperate regions of the world; adventive from Europe.

Brassica hirta Moench. [*Sinapsis alba* L.; *B. alba* (L.) Rabenh., not Gilib.] Plants erect, pubescent with coarse, descending hairs at least below, the stems 2-10 dm tall, usually branched; basal leaves lyrate-pinnatifid, mostly 5-15 cm long, the terminal lobe 3-10 cm wide, obscurely crenate-dentate; cauline leaves reduced upwards, usually all petiolate, becoming merely lobed, not auriculate; pedicels 5-10 mm long, slender or stout, spreading, often hirsute; sepals 4-5 mm long, yellowish, glabrous; petals 7-10 mm long, yellow; siliques (20) 30-50 mm long, 3-4.5 mm wide, the beak 8-16 mm long, 3 (5) nerved, the valves conspicuously 3-nerved, hirsute.— Cultivated white mustard of commerce and rarely escaping, but potentially a noxious weed of cultivated land and to be expected in agricultural regions of the state; widespread in the western United States; adventive or introduced from Europe.

Brassica juncea (L.) Czernj. [*Sinapsis juncea* L.] Indian Mustard. Plants erect, glabrous or hirsute, the stems 3-10 dm tall or more, usually branched; basal leaves lyrate-pinnatifid, 8-25 cm long, terminal lobe 5-15 cm wide, crenate to dentate or lobed; cauline leaves reduced upwards, short-petiolate to sessile, not auriculate-clasping;

pedicels 8-17 mm long, slender to stout, ascending, glabrous; sepals 4-6 mm long, yellowish, glabrous; petals (5.5) 7-12 mm long, yellow; siliques 20-50 mm long, 2-3 mm wide, beak 6-12 mm long, 1-veined, valves 1 (or lightly 3) nerved, glabrous.— A weed of disturbed soils (Washington County) but not yet common in the state; introduced from Asia.

Brassica kaber (DC.) Wheeler. [*Sinapsis arvensis* L.; *B. arvensis* Rabenh., not L.; *S. kaber* DC.] Charlock. Plants erect, pubescent with coarse spreading hairs at least below, stems 3-10 dm tall or more, simple or branched; basal leaves lyrate-pinnatifid to merely dentate, 5-20 cm long, 3-10 cm wide; cauline leaves reduced upwards, short-petiolate or sessile, not auriculate-clasping, or, if apparently so, falsely petiolate or leaves sinuate-dentate; pedicels 2-6 mm long, ascending, stout, glabrous; sepals 4-5 mm long, yellowish, glabrous; petals 8-14 mm long, yellow; siliques 30-50 mm long, 2-3 mm thick, beak 7-15 mm long, 3-veined, valves 3 (5)-nerved, glabrous.—Roadsides, fields, and ditch banks in Summit, Utah, and Washington counties, but probably in all counties of the state; widespread in temperate portions of the world; adventive from Europe.

Brassica nigra (L.) Koch in Röhling. [*Sinapsis nigra* L.] Black Mustard. Plants erect, glabrous or more usually sparsely to densely hirsute-hispid at least near base, stems 3-12 dm tall or more, usually branched; basal leaves lyrate-pinnatifid to lobed or serrate-dentate, 5-25 cm long, 2-15 cm wide; cauline leaves reduced upwards, short petiolate to sessile, not auriculate; pedicels 2-6 mm long, erect, stout, glabrous; sepals 3-4 mm long, yellowish, glabrous; petals (5) 7-12 (15) mm long, yellow; siliques 10-25 mm long, 1-2 mm wide, beak 1-5 mm long, 1-veined, valves with 1 midnerve and two faint lateral ones, glabrous.— Roadsides, fields, and other disturbed places in Garfield, Juab, Salt Lake, San Juan, Utah, Wasatch, Washington, Weber, and perhaps all Utah counties; widespread in North America; adventive from Europe.

This is a common weed of grainfields in northern Utah.

CAMELINA Crantz
False Flax

Plants pubescent with forked or stellate hairs, annual, from taproots; leaves alternate, simple, entire, auriculate-clasping basally; flowers racemose, pedicels ascending, not subtended by bracts; sepals 4, deciduous; petals 4, pale yellowish; stamens 6, filaments lacking glandular processes; styles slender, stigma capitate; fruit a silique, less than twice longer than broad, obovoid, somewhat compressed parallel to septum, valve 1-nerved; seeds several per locule, biseriate.

A Eurasian genus of 8-10 species.

Camelina microcarpa Andrz. ex DC. Plants erect, stems (0.8) 1.5-8 dm tall or more, hirsute to subappressed with simple and forked to stellate hairs at least near base; leaves mainly cauline, basal mostly 1-7 cm long, entire or obscurely toothed, usually withered by late anthesis; cauline leaves reduced upward, at least upper ones auriculate; pedicels spreading-ascending, (6) 8-18 mm long, glabrous; sepals 2-2.7 mm long, often reddish, more or less villous; petals 3-4 (5) mm long, white or nearly so, apex rounded; siliques 5-6.5 mm long, 3-4 mm wide, moderately inflated, glabrous; styles 1-2 (2.5) mm long, persistent.— Roadsides, foothills, gardens, and other disturbed moist to dry sites in Box Elder, Juab, Millard, Salt Lake, Summit, Tooele, Utah, and Weber counties; widespread in North America; adventive from Asia.

CAPSELLA Medic.
Nom. Cons.

Plants stellate-pubescent and often with coarse simple hairs also, annual, from taproots; leaves alternate or basal, simple, dentate or variously toothed or lobed to entire, cauline ones auriculate-clasping; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white; stamens 6, the filaments lacking glandular processes; style short, stigma capitate; fruit a silicle, less than twice longer than broad, cuneate-obcordate in outline, compressed at right angles to the septum, valves reticulately veined, strongly keeled; seeds many per locule.

A genus of European plants of perhaps 5 species, now widely disseminated as weeds.

Capsella bursa-pastoris (L.) Medic. [*Thlaspi bursa-pastoris* L.; *Bursa pastoris* Weber in Wigg.; *Bursa bursa-pastoris* (L.) Britton] Sheperd's Purse. Plants erect, stems 1-5 dm tall, stellate pubescent and more or less hirsute; basal leaves oblanceolate in outline, 2.5-16 (20) cm long, 0.5-2.8 (4) cm wide, lyrate-pinnatifid to merely toothed or subentire; cauline leaves much reduced upwards, sessile and auriculate; sepals 1.2-2.5 mm long, often reddish, pubescent or glabrous; petals 2-4 mm long, white to pinkish, apex rounded; silicles 4.5-8 mm long, 3-5 (6) mm wide, cuneate-obcordate, glabrous; styles 0.3-0.6 (1) mm long, persistent.— Disturbed sites at low to moderate elevations in Cache, Garfield, Juab, Kane, Salt Lake, Uintah, Utah, Wasatch, Washington, and Weber counties (probably in all counties); widespread in North America; introduced from Europe.

We may have, in our material from Utah, two other species from Europe which are infrequently recognized: Flowers pinkish (*C. rubella* Reuter) and a white flower form with the style 0.5-1 mm long (*C. thracica* Velen.).

CARDAMINE L.
Bitter Cress

Plants glabrous or sparsely pubescent with simple hairs, annual, biennial, or perennial from taproots or rhizomes; leaves alternate, sometimes with basal rosettes, simple to pinnately compound, petiolate, not auriculate; flowers racemose or rarely subcorymbose, pedicels spreading-ascending to ascending, not subtended by bracts; sepals 4, deciduous; petals 4, white to pinkish; stamens 6, filaments lacking glandular processes; style stout, stigma capitate; fruit a silique, several to many times longer than broad, slightly compressed parallel to septum, valves obscurely 1 (3)-nerved or nerveless; seeds several to many, uniseriate.

A genus of perhaps 150 species of the north temperate regions of the world.

Schulz, O. E. 1903. Monographie der Gattung *Cardamine*. Bot. Jahrb. Syst. 32: 280-623.

1. Leaves all simple, cordate-ovate to orbicular; petals 7-12 mm long; plants of stream and seep margins at middle and higher elevations .... *C. cordifolia*
   Leaves pinnately compound, at least the lower ones; petals 2-7 mm long; plants of spring and seep margins, occasionally elsewhere, at middle to low elevations 2

2(1). Leaflets usually 3-5, terminal leaflet, at least, more than 10 mm wide; upper leaves simple, with broadly ovate blades; petals 3-7 mm long; siliques 1-2 mm wide .... *C. breweri*
   Leaflets usually 6-11 (rarely 3-5), terminal leaflet usually less than 10 mm wide; upper leaves compound; petals 2-3 mm long; siliques 0.7-1 mm wide 3

3(2). Cauline leaves mostly 2-4 cm long, with narrow nondecurrent lateral segments 1-3 mm wide, linear to linear-spatulate or narrowly oblong; rare .... *C. parviflora*
   Cauline leaves mostly 4-8 cm long, with broad decurrent lateral segments 3-8 mm wide, commonly oval to broadly oblong; infrequent .... *C. pensylvanica*

Cardamine breweri S. Wats. [*C. vallicola* Greene] Plants perennial, rhizomatous, erect or descending, stems (2) 2.5-5 (6) dm tall, glabrous or pubescent with simple hairs near the base; leaves mostly cauline, pinnately compound with 3-5 (rarely more in ours) leaflets, or basal and upper ones simple, mostly 1-7 cm long, lateral leaflets mostly 10-25 mm long and 0.4-1.2 mm wide, terminal segment 12-35 mm long and 13-30 mm wide, subentire to sharply toothed, ovate to orbicular, glabrous or sparsely hirsute; pedicels 4-10 mm long or more, glabrous, ascending; sepals 1.5-2.5 mm long, whitish, glabrous or sparingly simple-hairy; petals 3-7 mm long, white, rarely pinkish, spatulate-obovate, spreading; siliques 17-30 mm long, 1-1.8 mm wide, erect or ascending, valves glabrous, obscurely 1 (3)-nerved; styles 0.5-2 mm long, tapering to stigma; seeds 1-1.5 mm long, smooth.— Stream sides and seep margins at middle elevations in Wasatch and Utah counties, and undoubtedly elsewhere; Alaska and British Columbia south to California, Nevada, Utah, and Colorado. Our plant is var. *breweri*.

Cardamine cordifolia A. Gray. [*C. cordifolia* var. *pubescens* A. Gray; *C. infausta* Greene; *C. uintahensis* F. J. Hermann] Plants perennial, rhizomatous, erect or ascending, stems (1.5) 2-6 dm tall, glabrous to more or less densely pubescent with simple hairs near the base; leaves mostly cauline, all simple, the blade mostly (1.5) 2-6 (8) cm long and 1.3-5 (7) cm wide, cordate-ovate or broader, usually sinnate-crenate, glabrous or rarely pubescent; pedicels mostly 10-20 mm long, glabrous or hairy, ascending-spreading; sepals 3-5 mm long, greenish, glabrous or sparingly hairy; petals 7-12 mm long, white, obovate-spatulate, spreading; siliques 20-35 mm long, (1) 1.5-3 mm wide, ascending to erect, valves glabrous, obscurely 1-nerved; styles 0.5-2 mm long or more; seeds 1.5 mm long or more, smooth.— Stream sides and seeps at middle to higher elevations in Beaver (US), Duchesne (US), Garfield (US), Iron, Piute, Salt Lake, San Juan (US), Sanpete (US), Sevier (US), Summit, Utah, Wasatch, Washington, Wayne (US), and Weber counties, and to be expected elsewhere; British Columbia to Wyoming south to California, Nevada, Utah, and New Mexico. Our plants is var. *cordifolia*.

Cardamine parviflora L. Plants annual or biennial from a taproot, stems erect, usually solitary, 1-3 dm tall, glabrous; basal leaves with 3-5 pairs of oblong to cuneate-obovate leaflets, lateral leaflets 0.2-0.4 (0.5) cm long and 0.2-0.3 cm wide, entire or slightly lobed, terminal leaflet broadly cordate to orbicular, 0.3-0.8 (1) cm long and 0.5-1 (1.2) cm wide; cauline leaves reduced upwards, mostly 2-4 cm long, with 3-6 pairs of lateral leaflets, segments similar to basal ones only lateral leaflets slightly narrower,linear to linear-spatulate or narrowly oblong, terminal segment linear to cuneate-oblong, entire or toothed, 0.5-1.2 cm long and 0.1-0.3 cm wide, not decurrent; pedicels 3-7 mm long, spreading-ascending, glabrous; sepals 1.2-1.6 mm long, greenish, glabrous; petals 2-3 mm long, white, oblanceolate, spreading; siliques 12-30 mm long, 0.5-1 mm wide, erect or nearly so, glabrous, style 0.3-0.6 mm long; seeds 1-1.5 mm long, smooth.— Rare and local, Duchesne County; widespread and common in the eastern United States; Europe. Our plant is var. *arenicola* (Britton) O. E. Schulz.

Cardamine pensylvanica Muhl. ex Willd. [*C. flexuosa* ssp. *pensylvanica* (Muhl.) Schulz; *C. hirsuta* var. *pensylvanica* (Muhl.) Graff] Plants annual or biennial from a taproot, stems erect, usually solitary, 1.5-3.5 dm tall, glabrous or pubescent; basal leaves with 7-11 pairs of oval to lanceolate or oblanceolate leaflets, lateral leaflets 0.3-1.5 cm long and 0.2-1.2 cm wide, entire or lobed, terminal leaflet orbicular to cuneate-oblanceolate, 0.4-2 cm long and 0.3-1.5 cm wide; cauline leaves reduced upwards, mostly 4-8 cm long, with 3-5 pairs of lateral leaflets, segments broadly oblong to oval, terminal segment cuneate-obovate, entire or toothed, (0.5) 1-3 cm long and 0.5-2 cm wide, decurrent; pedicels 3-10 mm long, spreading-ascending, glabrous; sepals 1.2-1.8 mm long, pinkish, glabrous; petals 2-3 mm long, white, oblanceolate, spreading; siliques 15-30 mm long, 0.7-1 mm wide, erect, glabrous, style 0.4-0.8 mm long; seeds 1-1.5 mm long, smooth.— Stream sides and other moist areas at middle to low elevations in Duchesne and Summit counties; widespread in North America.

This species is only weakly distinct from *Cardamine oligosperma* Nutt. ex Torr. and Gray, and that species might better be treated as a variant of *C. pensylvanica*. The difficulty with this proposal is that *C. pensylvanica* itself may only be a minor phase of the European *C. hirsuta* L. We cannot express an opinion on the taxonomy of this species complex based upon our provincial studies, but suspect that our material might best be considered a subspecies of the European plant based upon what we have seen in herbaria.

CARDARIA Desv.

White-top

Plants pubescent rhizomatose perennials; leaves alternate, sinuate-dentate, auriculate-clasping; flowers in clustered (paniculate) racemes, pedicels spreading-ascending, not subtended by bracts; sepals 4, caducous; petals 4, yellow, the apex rounded; stamens 6, filaments lacking glandular processes; style slender, prominent, stigma capitate; fruit a silicle, usually broader than long, compressed at right angles to septum, indehiscent or tardily so, valves reticulately veined; seeds 1 (rarely 2) per locule.

As here defined, a genus of 4 species of Europe and Asia.

Rollins, R. C. 1940. On two weedy crucifers. Rhodora 42: 302-306.

1. Silicles obcordate in outline, glabrous; plants widespread and common .... *C. draba*
Silicles orbicular in outline, pubescent or glabrous; plants uncommon 2

2(1). Silicles puberulent, 1.5-2.5 mm long and about as wide .... *C. pubescens*
Silicles glabrous, 3-4 mm long and about as wide .... *C. chalepense*

Cardaria chalepensis (L.) Hand.-Mazz. [*Lepidium chalepense* L., *L. draba* ssp. *chalepense* (L.) Thell., *C. draba* ssp. *chalepensis* (L.) O. E. Schulz] Plants decumbent to ascending or erect, 2-6 dm tall, glabrous; leaves elliptic to oblong or lanceolate, 0.8-10 cm long, 0.3-2 cm wide, sinuate-dentate to entire, the upper sessile and auriculate; pedicels 2-8 mm long in fruit, spreading-ascending, glabrous; sepal 1.2-1.8 mm long, greenish to whitish, glabrous; petals 2-3 mm long, white, spatulate, spreading; silicles (excluding the style) 3-4 mm long, 3-4 mm wide, erect, glabrous, style 0.7-1 mm long; seeds 1 or 2. Moist soil, at 1500 to 1700 m in the Oquirrh Mountains, Salt Lake Co. (Rokich s.n. UT, BRY), and to be expected elsewhere; adventive from Europe.

Cardaria draba(L.) Desv. [*Lepidium draba* L.; *Cochlearia draba* (L.) L. *Physolepidium repens* Schrenk ex Fisch. and Meyer; *L. repens* (Schrenk) Boiss.; *C. repens* (Schrenk) Jarmolenko] Plants decumbent to ascending or erect, stems (1.2) 1.5-6 dm tall, puberulent to hirtellous with usually descending simple hairs; leaves elliptic to oblong, ovate, or oblanceolate, 0.9-9.8 cm long, 0.6-3.5 cm wide, sinnate-dentate to irregularly toothed, lower ones petiolate, upper sessile and auriculate, puberulent to hirtellous with usually retrorse simple hairs; pedicels 5-12 mm long in fruit, spreading-ascending, glabrous or puberulent; sepals 1.2-2 mm long, greenish, usually glabrous; petals 2-3.5 (4) mm long, white, broadly spatulate, spreading; silicles (excluding the style) 2-3.8 mm long, 3.5-5.7 mm wide, erect, glabrous, style 0.6-1.2 mm long; seeds 1-2 mm long.— Cultivated and waste places at lower elevations in Beaver, Duchesne, Juab, Salt Lake, Sanpete, Sevier, Utah, Washington, and Weber counties (and probably in most counties of the state); widespread in the United States and Canada; adventive from Europe.

Cardaria pubescens (C. A. Meyer in Ledeb.) Jarmolenko. [*Hymenophysa pubescens* C. A. Meyer in Ledeb.] Plant ascending to erect, stems 1.5-4 dm tall, puberulent to hirtellous with usually descending simple hairs; leaves elliptic to oblong or oblanceolate, 0.6-6 cm long, 0.3-1.5 cm wide or longer, irregularly sinuate-dentate, the lower petiolate, upper sessile and auriculate, puberulent to hirtellous with usually simple hairs; pedicels 6-10 mm long in fruit, ascending, hairy; sepals 1.8-2 mm long, greenish, hairy; petals 3.5-4 mm long, white, broadly spatulate, spreading; silicles (excluding the style) 1.5-2.5 mm long and about as wide, erect, puberulent, style 0.7-1.2 mm long.— Agricultural lands and disturbed places, Salt Lake Co., and to be expected elsewhere; widespread in the United States and Canada; adventive from Asia. Our plants are var. *elongata* Rollins.

As here defined, the genus *Cardaria* includes *Hymenophysa*. Except for an occasional publication, this seems to be strictly an American concept as most workers in Europe and Asia prefer to distinguish between the two.

CAULANTHUS S. Wats.

Plants glabrous or pubescent with simple hairs, rarely with some malpighian ones, annual to perennial, from taproots; leaves alternate or mostly basal, simple, lyrate-pinnatifid, pinnatifid, toothed or subentire, petiolate or sessile and auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white, yellow, or chestnut-brown to purple; stamens 6, filaments lacking glandular processes; style obsolete or slender and conspicuous, stigma capitate and sometimes distinctly bilobed; fruit a sessile or subsessile silique, many times longer than broad, terete or more or less compressed, valves 1 (3)-nerved; seeds several to many, uniseriate.

A genus of 10-12 species of the western United States, and mainly of California.

Payson, E. B. 1922. A monographic study of *Thelypodium* and its immediate allies. Ann. Missouri Bot. Gard. 9:233-324.

Rollins, R. C. 1971. Protogyny in the Cruciferae and notes on *Arabis* and *Caulanthus*. Contr. Gray Herb. 201:3-10.

1. Cauline leaves sessile and auriculate at the base; plants of southwestern Utah . ... *C. cooperi*
   Cauline leaves petiolate or sessile but not auriculate; plants of broad distribution and sometimes of southwestern Utah 2

2(1). Stems usually conspicuously inflated, glabrous or nearly so; plants perennial ... . *C. crassicaulis*
   Stems not inflated; hispid (at least below); plants annual or biennial 3

3(2). Pedicels very short, 1-2 mm long, soon recurved; siliques up to 4 cm long, descending; known only from Washington County .... *C. lasiophyllus*
   Pedicels 3-7 mm long, spreading-ascending; siliques 4.5-13.5 cm long, ascending to curved-pendulous; known only from Millard and Tooele counties.. *C. pilosus*

Caulanthus cooperi (S. Wats.) Payson. [*Thelypodium cooperi* S. Wats.; *Guillenia cooperi* (S. Wats.) Greene] Plants annual, erect or sprawling, stems not inflated, 1-7.5 dm tall, glabrous and often glaucous or sparsely pubescent with simple or malpighian hairs; leaves mainly cauline, lower ones 1-7 cm long, 0.4-2 cm wide or more, obscurely sinuate-dentate, glabrous, cauline ones reduced upwardly, mostly 1-7.5 cm long and 0.2-1.2 cm wide, mostly entire with at least the uppermost auriculate; pedicels 1-4 mm long, soon recurved, glabrous; sepals 5-6.5 (7) mm long, green or reddish, glabrous; petals 6-9 mm long, yellowish, suffused with purple, narrowly spatulate, ascending; anthers 1-1.3 mm long; siliques 20-45 mm long, 2-3 mm wide, sessile, descending, compressed, glabrous; styles 1-2.5 mm long, stigma not expanded, shortly bilobed.— *Larrea* and Joshua tree communities in Washington County, Utah; Arizona, Nevada, and California.

Caulanthus crassicaulis (Torr.) S. Wats. Plants perennial, erect, stems usually strongly inflated, (2) 3.2-9.7 (10.8) dm tall, glabrous and glaucous; leaves mainly basal, lower ones 3-12 (17) cm long, 0.3-3 cm wide, lyrate-pinnatifid to entire, glabrous, cauline ones much reduced upwardly, linear to narrowly oblanceolate, petiolate and not auriculate; pedicels 1-4 mm long, stout, ascending, glabrous or more commonly hirsute at least apically; sepals (7) 9-13 mm long, brown to brown-purple, narrowly spatulate, spreading-ascending; anthers 3.9-6.3 mm long; siliques 70-140 mm long, 1.5-2 mm wide, sessile, ascending to erect, glabrous; style obsolete, stigma more or less expanded, lobes up to 0.8 mm long.—

Pinyon-juniper, sagebrush, shadscale, and ponderosa pine woodlands from moderate to low elevations in the southern two-thirds of Utah; Oregon and Idaho to Colorado south to California and Arizona.

As here defined, we are treating *Caulanthus crassicaulis* in a broad sense and not recognizing *C. glaber* nor *C. major*. These three sympatric entities, segregated on features which tend to show some apparent intergradation in Utah, seem to be very distinct elsewhere, particularly in Nevada and California. The var. *crassicaulis* is reported to have a haploid number of $n = 12$, whereas as one of us has shown (Reveal & Styer, Southw. Naturalist 18:397-402. 1974) the var. *glaber* is $n = 14$ based on a collection from southwestern Nevada. The two variants of the species must be carefully investigated in the field to see if the plants found outside Utah really belong to the taxa we have in the state.

1. Sepals more or less hirsute; plants of broad distribution .... C. *crassicaulis* var. *crassicaulis*
Sepals glabrous or with a few hairs; plants of various distributions 2

2(1). Stigmas deeply divided; plants common .... *C. crassicaulis* var. *glaber*
Stigmas shallowly lobed; plants evidently rare .... *C. crassicaulis* var. *major*

Var. ***crassicaulis.*** [*Streptanthus crassicaulis* Torr.; *C. senilis* Heller] Widespread and locally common in Box Elder, Carbon (US), Daggett, Duchesne, Emery, Juab, Kane, Sanpete, Sevier, and Uintah (US) counties and likely elsewhere—the type is from the east side of the Great Salt Lake; Idaho, Nevada, Colorado, Arizona, and California.

Var. ***glaber*** M. E. Jones. [*C. glaber* (M. E. Jones) Rydb.] Widespread and locally common in Beaver, Garfield, Kane, Millard, Piute, San Juan, Sevier, and Washington counties—the type is from Sink Valley in Kane County; southern Nevada.

Var. ***major*** M. E. Jones [*C. major* (M. E. Jones) Payson; *C. procerus* of authors, not S. Wats.] Rare and local, perhaps not separable from var. *glaber* in Utah where known only from Garfield County—the type is from Bromide Pass in Henry Mountains; Nevada and California where perfectly distinct from both var. *glaber* and var. *crassicaulis.*

Caulanthus lasiophyllus (Hook. & Arn.) Payson. [*Turritis lasiophylla* Hook. & Arn.; *Thelypodium lasiophyllum* (Hook. & Arn.) Greene; *Sisymbrium lasiophyllum* (Hook. & Arn.) K. Brandegee; *Guillenia lasiophylla* (Hook. & Arn.) Greene] Plants annual, stems not inflated, 1-8 (12) dm tall, more or less hirsute with simple or rarely forked hairs; leaves mainly cauline, these 0.7-15 cm long, 0.1-5.5 cm wide, irregularly pinnatifid, petiolate and not auriculate; pedicels 1-2 mm long, deflexed in fruit, glabrous or sparingly hirsute; sepals 2-3 mm long, often purplish, glabrous; petals 3-5 mm long, yellowish, oblong-spatulate, not constricted at juncture of blade and claw, ascending-spreading; anthers 0.6-1 (1.5) mm long; siliques 25-45 (60) mm long, 0.8-1.1 mm wide, sessile, terete, reflexed-descending, glabrous; styles 0.8-1.3 mm long, stigma small, obscurely lobed.— Sandy or gravelly soils in the *Larrea* community in Washington County; California and Nevada south into Arizona and Mexico. Our material has been designated as var. *utahensis* (Rydb.) Payson [*Thelypodium utahense* Rydb.; *T. lasiophyllum* var. *utahense* (Rydb.) Jeps.], basically a Mojave Desert phase which occurs in northwestern Arizona, southern Nevada, and southeastern California.

Caulanthus pilosus S. Wats. [*Streptanthus pilosus* (S. Wats.) Jeps.] Plants biennial or infrequently annual, stems not inflated, mostly 4-10 dm tall or more, hirsute with simple hairs at least below; leaves mostly basal, lower ones 3-15 cm long, 0.5-3.5 cm wide, irregularly pinnatifid, hirsute, cauline ones only slightly reduced and shorter upwardly, petiolate and not auriculate; pedicels 4-9 mm long, spreading-ascending, glabrous or nearly so; sepals 5-7 (9) mm long, often purplish, glabrous or hairy; petals 7.5-9 (10) mm long, white, suffused with purple or pink, spatulate-lanceolate, constricted at juncture of blade and claw, ascending-spreading; anthers 2-4 mm long; siliques 70-115 mm long, 0.8-1 (1.5) mm wide; style short, stigma bilobed.— Sandy or gravelly soils in the shadscale-winter fat communities of Millard and Tooele counties; Oregon and Idaho south to California and Nevada.

CHLOROCRAMBE Rydb.

Plants glabrous perennials from a stout caudex; leaves alternate and mainly cauline, simple, more or less hastate, entire or sinuately lobed, petiolate, not both sessile and auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white; stamens 6, filaments lacking glandular processes; style obsolete or up to 0.5 mm long, stigma small, entire; fruit a stipitate silique, many times longer than broad, subterete, valves 1 (3-5)-nerved; seeds uniseriate.

A monotypic genus.

Chlorocrambe hastatus (S. Wats.) Rydb. [*Caulanthus hastatus* S. Wats.] Plants erect, stems 6-18 dm tall, usually simple, glabrous and glaucous; leaves with slender petioles 1-16 cm long, blades hastate to ovate or lanceolate, 3-13.5 cm long, 1-8.5 cm wide, more or less hastate, entire or sinuate-lobed; pedicels spreading to reflexed, 5-10 mm long, glabrous; sepals usually surpassing petals, their tips coiled, yellowish-green, glabrous; petals 4.5-8 mm long, white, mostly 4-6 mm long, blade constricted at juncture with claw, ascending-spreading; siliques 40-105 mm long, 1.8-2.5 mm wide, spreading to curved descending, glabrous, stipe 2-7 mm long; style up to 0.5 mm long, stigma not lobed.— Thickets, woodlands, and less commonly in openings from 1900 to 2800 m elevation in Davis, Salt Lake, Tooele, Utah, Wasatch, and Weber counties; known only from northern Utah and the Wallowa Mountains of northeastern Oregon.

CHORISPORA R. Br.
ex DC. Nom. Cons.

Plants stipitate-glandular and infrequently also hirsute annuals, from taproots; leaves alternate and basal, simple, sinuate-dentate to pinnatifid or entire, cauline ones petiolate to sessile but not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, pink to lavender; stamens 6, filaments lacking glandular processes; style apical on a slender sterile beak, stigma minute, bilobed; fruit a silique, many times longer than broad, terete, indehiscent, breaking at maturity into 1-seeded segments, valves 1 (3 or more)-nerved; seeds uniseriate.

A genus of about 9 species, mainly of central Asia.

Chorispora tenella (Pall.) DC. [*Raphanus tenellus* Pall.; *Chorispermum tenellum* (Pall.) R. Br. ex Ait.] Plants decumbent-ascending to erect, stems 0.2-4.5 dm tall, simple or branched from base, stipitate-glandular and often simple hirsute at least at base; leaves mainly cauline, 0.5-8.5 cm long, 0.1-2.8 cm wide, sinuate-dentate, pinnatifid, or entire, petiolate or sessile but not auriculate; pedicels spreading-ascending, 2-6 mm long, stipitate-glandular and often sparingly hirsute; sepals 4.4-6.7 mm long, reddish or purplish, stipitate-glandular; petals 9-12.5 mm long, pink to lavender, apex rounded, spreading; siliques 30-45 mm long, curved-ascending, stipitate-glandular, beak 8-22 mm long; style obsolete or very short, stigma minute.— Roadsides, foothills, and other disturbed sites at lower elevations in Box Elder, Emery, Grand, Kane, Salt Lake, Sanpete, Utah, Washington, Wayne, and Weber counties, and probably throughout the state; Washington and Idaho south to California, Arizona and Colorado; adventive from Asia.

CONRINGIA Adans.

Plants glabrous and glaucous annuals or biennials, from taproots; leaves alternate and basal (and still alternate), simple, entire, tapering to base or cauline sessile and auriculate-clasping; flowers racemose, pedicels ascending to curved-erect, not subtended by bracts; sepals 4, deciduous; petals 4, yellow or cream; stamens 6, filaments lacking glandular appendages; styles stout, stigma lobed; fruit a sessile, slender silique many times longer than broad, quadrangular, valves 1—3-nerved; seeds numerous, uniseriate.

About 6 species of Eurasia.

Conringia orientalis (L.) Dumort. [*Brassica orientalis* L.] Hare's-ear Mustard. Plants annual or winter annual, stems 1.9-5 (7) dm tall, solitary or 2 or 3 from base, glabrous; basal leaves 3-6 (9) cm long, 1.2-3 cm wide, entire, glabrous; cauline leaves several, 1.7-12 cm long, 0.8-5.7 cm wide, ovate to oblong to elliptic, shorter to longer than internodes, glabrous, entire; pedicels 5-14 mm long, ascending to curved-erect, glabrous; sepals 4.3-6 (8) mm long, glabrous, often reddish tinged, acute; petals 6.2-10 (12) mm long, yellow to cream, spatulate, spreading-ascending; siliques 70-100 (130) mm long, 1.5-2 mm thick, erect, valves glabrous; styles up to 1 mm long, stigma small; seed numerous.— Slopes, roadsides, and other disturbed sites at middle and lower elevations in Utah and Washington counties (and to be expected elsewhere); widely distributed in North America; adventive from Europe.

DESCURAINIA Webb and Berthel.
Nom. Cons.

Plants stellate-pubescent, stipitate-glandular, or glabrate annuals or biennials from slender to stout taproots; leaves basal and cauline, alternate, 1-3 times pinnately compound or pinnatifid, not auriculate basally; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow to cream; stamens 6, filaments lacking glandular processes; style short or obsolete, stigma capitate; fruit a silique more than (3) 5 times longer than broad, linear to oblong or clavate, terete or nearly so, valves 1-nerved, glabrous; seeds several to many, uniseriate or biseriate.

Perhaps 30 species mainly of the Americas, a few in Europe.

Detling, L. E. 1939. *Descurainia* in North America. Amer. Midl. Naturalist 22:481-520.

Schulz, O. E. 1924. *Descurainia*. Pflanzenr. IV. 105 (Heft 86): 481-520.

1. Upper leaves bi- or tripinnate; siliques narrowly linear, mostly about 20 (10-30) mm long; seeds usually more than 20, uniseriate; replum 2-3-nerved; tall to low plants of low elevations .... *D. sophia*
Upper leaves once-pinnate; siliques clavate, elliptic, or, if linear, less than 20-seeded and less than 15 mm long; replum nerveless or 1-nerved 2

2(1). Siliques clavate or linear to elliptic, rounded to pointed above; seeds often in 2 rows or at least partially so; replum usually nerveless; plants of middle to lower elevations .... *D. pinnata*
Siliques linear or elliptic, usually pointed above; seeds in one row; replum 1-nerved; plants of middle and higher elevations 3

3(2). Siliques 7-14 mm long, linear or less commonly ellipsoid; pedicels appressed-erect or ascending; seeds mostly 4-10 per locule .... *D. richardsonii*
Siliques 3.3-7.2 mm long, ellipsoid; pedicels ascending to spreading; seeds mostly 1-3 per locule .... *D. californica*

Descurainia californica (A. Gray) O. E. Schulz. [*Smelowskia californica* A. Gray] Plants annual or winter annual to biennial, stems 4-13 dm tall or more, simple or more commonly profusely branching from most of upper leaf and bract axils, minutely dendritic-stellate pubescent to almost or quite glabrous below, glabrous above; leaves basal and cauline, 2-7 cm long, lower once-pinnately compound with 2-4 pairs of entire to incised pinnae, upper reduced, once-pinnate or pinnatifid; pedicels 3-7 mm long, spreading to spreading-ascending, glabrous; sepals spreading, 0.8-1.3 mm long, yellow or greenish, glabrous; petals 1.1-1.6 mm long, yellow; siliques 3.3-7.2 mm long, 0.9-1.3 mm wide, erect or ascending, not appressed; styles 0.3-0.7 mm long; seeds uniseriate, 1-3 per locule.— Woodlands, especially in aspen but also in ponderosa pine, spruce-fir, and less commonly in mountain brush communities from 1750 to 3100 m elevation in Beaver, Carbon, Garfield, Millard, Piute, Salt Lake, Utah, Washington, Wayne, and Weber counties; Wyoming, Colorado, and New Mexico westward to California.

This taxon is a mirror-image congener of *Descurainia richardsonii* (q.v.), especially of those taxa of that species with ascending pedicels.

Descurainia pinnata (Walter) Britton [*Erysimum pinnatum* Walter; *Sisymbrium pinnatum* (Walter) Greene; *Sophia pinnata* (Walter) Howell] Pinnate Tansy-Mustard. Plants annual or winter annual, stems 1-10 dm tall, stellate-pubescent and sometimes also stipitate-glandular at least below, simple or highly branched above; leaves basal and cauline, 2-10 cm long, once to twice pinnatifid, segments linear to oblong, often toothed, upper reduced and usually once pinnatifid; pedicels 3-24 mm long, spreading, stellate-pubescent to glabrous; sepals 1-2.2 mm long, yellowish to greenish or violet, stellate-pubescent to glabrous; petals 1.5-3 mm long, cream to yellow; siliques 3-15 (rarely 20) mm long, 1-2 mm wide, clavate to oblong or linear, very rarely ellipsoid; styles up to 0.3 mm long; seeds 1-20 per locule, biseriate in part.—Widespread and common in arid to submesic regions of North America; composed of numerous freely intergrading variants, several of which occur in Utah.

1. Pedicels (17) 18-24 mm long; siliques mostly 12-18 mm long; petals yellow, over 2 mm long; terminal leaflet of uppermost leaves linear, entire, and more than 2 cm long; plants of Grand, San Juan, and Uintah counties .... *D. pinnata* var. *paysonii*
   Pedicels usually less than 15 mm long; siliques often less than 12 mm long (up to 20 mm in var. *filipes*); terminal leaflet various but not or seldom as above; petals yellow to cream, shorter or longer than 2 mm in length; distribution various 2

2(1). Stems moderately to densely stipitate-glandular 3
   Stems stellate-pubescent to glabrous, not at all stipitate-glandular 4

3(2). Flowers with calyx usually rose-colored; corolla 1.5-2 (2.2) mm long; siliques usually 10 mm long or less .... *D. pinnata* var. *osmiarum*
   Flowers with calyx yellowish; corolla 2-3 mm long; siliques often more than 10 mm long .... *D. pinnata* var. *filipes*

4(2). Siliques usually shorter than pedicels, mostly 10-21 mm long, not or only somewhat clavate in outline .... *D. pinnata* var. *osmiarum*
   Siliques usually subequal to or longer (rarely shorter) than pedicels, mostly 3-12 mm long, more or less clavate or elliptic in outline 5

5(4). Siliques 3-8 mm long, borne on pedicels 4-12 mm long; plants of warm deserts in Washington County .... *D. pinnata* var. *glabra*
   Siliques 8-10 mm long, or, if only 4-8 mm long, not of Washington County; pedicels various 6

6(5). Pedicels 4-6 (8) mm long; flowers 1-1.5 mm long .... *D. pinnata* var. *nelsonii*
   Pedicels (6) 8-12 mm long; flowers 2-3 mm long .... *D. pinnata* var. *intermedia*

Var. ***filipes*** (A. Gray) M. E. Peck. [*Sisymbrium incisum* var. *filipes* A. Gray; *Sisymbrium longipedicellata* Fourn. *Sophia filipes* (A. Gray) Heller; *Sisymbrium gracilis* Rydb.; *D. rydbergii* var. *eglandulosa* O. E. Schulz; *D. longipedicellata* (Fourn.) O. E. Schulz; *D. longipedicellata* var. *glandulosa* O. E. Schulz; *Sisymbrium glandifera* Osterh.; *Sisymbrium longipedicellata* var. *glandulosa* (O. E. Schulz) St. John; *D. pinnata* ssp. *filipes* (A. Gray) Detling] Common and widespread from 975 to 2300 m elevation in desert shrub, mountain brush, pinyon-juniper, and ponderosa pine communities in

Beaver, Emery, Grand, Juab, Kane, Millard, Salt Lake, San Juan, Sevier, Tooele, Utah, Washington, and Wayne counties; British Columbia and Alberta south to California, Arizona, and Colorado.

Var. ***glabra*** (Woot. & Standl.) Shinners. [*Sophia glabra* Woot. & Standl.; *D. pinnata* ssp. *glabra* (Woot. & Standl.) Detling] Local common from 750 to 1200 m elevation in Washington County; Arizona and New Mexico west to California and northern Mexico.

Var. ***intermedia*** (Rydb.) C. L. Hitchc. [*Sophia intermedia* Rydb.; *D. intermedia* (Rydb.) F. P. Daniels; *Sisymbrium intermedium* (Rydb.) Garrett; *D. pinnata* ssp. *intermedia* (Rydb.) Detling] Locally common in pinyon-juniper, sagebrush, and semidesert shrublands from 1200 to 1850 m elevation in Garfield, Kane, Millard, Uintah, and Wayne counties; British Columbia and Alberta south to California, Nevada, Utah, and Colorado.

Var. ***nelsonii*** (Rydb.) M. E. Peck. [*Sophia nelsonii* Rydb.; *D. brachycarpa* var. *nelsonii* (Rydb.) O. E. Schulz] Widespread but apparently uncommon from 1200 to 3250 m elevation in Duchesne, Garfield, San Juan, Sevier, Uintah, and Wasatch counties; Washington east to Montana and south to Nevada, Utah, and Colorado.

Var. ***osmiarum*** (Cockerell) Shinners. [*Sophia andrenarum* var. *osmiarum* Cockerell; *S. halictorum* Cockerell; *S. andrenarum* Cockerell; *Sisymbrium halictorum* (Cockerell) K. Schum.; *D. halictorum* (Cockerell) O. E. Schulz; *D. halictorum* var. *andrenarum* (Cockerell) O. E. Schulz; *D. halictorum* var. *osmiarum* (Cockerell) O. E. Schulz; *D. andrenarum* (Cockerell) Cory; *D. pinnata* ssp. *halictorum* (Cockerell) Detling] Our most common variant, in sagebrush, pinyon-juniper, salt-desert shrub, grasslands, and warm desert shrublands from 850 to 2450 m elevations in Box Elder, Davis, Duchesne, Emery, Garfield, Iron, Juab, Kane, Millard, Piute, San Juan, Sevier, Uintah, Utah, Washington, and Wayne counties; Oregon to Wyoming south to Mexico, Oklahoma, and Arkansas.

Var. ***paysonii*** (Detling) Welsh & Reveal, stat. nov., based on *Descurainia pinnata* ssp. *paysonii* Detling, Amer. Midl. Naturalist 22:515. 1939. Uncommon in pinyon-juniper and sagebrush zones at lower elevations in Grand, San Juan, and Uintah counties; Wyoming and Colorado south into Arizona.

Descurainia richardsonii (Sweet) O. E. Schulz. [*Sisymbrium canescens* Richards., not *D. canescens* Nutt.; *S. richardsonii* Sweet; *S. canescens* var. *major* Hook.; *Sophia richardsoniana* Rydb.] Richardson Tansymustard. Plants annual or winter annual to biennial, stems (1.5) 3-12 dm tall or more, simple or more commonly profusely branching from upper leaf and bract axils, minutely dendritic-stellate pubescent and sometimes also minutely stipitate-glandular to almost or quite glabrous below, glabrous or glandular above; leaves basal and cauline, 1.5-8 cm long, the lower once- to twice-pinnatifid with 2-4 pairs of toothed or lobed or subentire pinnae, the upper reduced and only once-pinnatifid; pedicels (2.5) 3-9 mm long, spreading to erect, pubescent or glabrous; sepals spreading, 0.9-1.7 mm long, yellow or greenish, glabrous or hairy; petals 1.3-2.8 mm long, yellow; siliques 7-14 mm long, 0.8-1.2 mm wide, ascending or erect, often appressed; styles 0.2-0.6 mm long; seeds uniseriate, (1-3) 4-10 per locule.—Spruce-fir, aspen, mountain meadows, or sagebrush communities from 2150 to 2900 m elevation in central and eastern Utah; British Columbia and Alberta south to California, Arizona, and Mexico. Three weakly defined variants can be at least arbitrarily distinguished as in the following key:

1. Pedicels and siliques erect, more or less appressed to raceme axis .... *D. richardsonii* var. *brevipes*
Pedicels ascending, siliques erect or ascending, neither one appressed to raceme axis 2

2(1). Plants not glandular .... *D. richardsonii* var. *sonnei*
Plants stipitate-glandular .... *D. richardsonii* var. *viscosa*

Var. *brevipes* (Nutt. ex Torr. & Gray) Welsh & Reveal, comb. nov., based on *Sisymbrium canescens* var. *brevipes* Nutt. ex Torr. & Gray, Fl. N. Amer. 1:92. 1838. [*Sophia procera* Greene; *Sisymbrium procerum* (Greene) K. Schum; *Sophia brevipes* (Nutt.) Rydb.; *D. richardsonii* var. *macrosperma* O. E. Schulz, type from Alta, Salt Lake County; *D. richardsonii* ssp. *procera* (Greene) Detling; *D. richardsonii* var. *procera* (Greene) Breitung] Locally common from 2450 to 2900 m elevation in Duchesne, Garfield, Iron, Piute, Salt Lake, Summit, and Wasatch counties; Idaho and Montana south to New Mexico.

Var. *sonnei* (B. L. Robinson) C. L. Hitchc. [*Sisymbrium incisum* Engelm. in Gray; *D. incisa* (Engelm.) Britton; *S. incisum* var. *sonnei* B. L. Robinson; *Sophia sonnei* (B. L. Robinson) Greene; *Sophia incisa* (Engelm.) Greene; *Sophia leptophylla* Rydb.; *Sophia serrata* Greene; *Sophia purpurascens* Rydb; *Sisymbrium leptophyllum* (Rydb.) Nels. & Macbride; *D. serrata* (Greene) O. E. Schulz; *D. incisa* var. *leptophylla* (Rydb.) O. E. Schulz; *D. richardsonii* ssp. *incisa* (Engelm.) Detling] Widespread and locally common from 1800 to 2750 m elevation in Duchesne, Garfield, Grand, Salt Lake, Utah, and Wasatch counties; Idaho and Montana southward to Mexico.

This phase of *Descurainia richardsonii* closely simulates *D. californica* (q.v.).

Var. *viscosa* (Rydb.) M. E. Peck. [*Sophia viscosa* Rydb.; *Sisymbrium viscosum* (Rydb.) Blankinship; *D. rydbergii* O. E. Schulz; *D. richardsonii* ssp. *viscosa* (Rydb.) Detling] Local and common from 2450 to 2900 m elevation in Duchesne and Wasatch counties; British Columbia and Alberta south to California, Arizona, and New Mexico.

The var. *richardsonii* is known to occur just north and east of Utah in southwestern Wyoming and northwestern Colorado. It differs from var. *brevipes* in being canescent as opposed to the moderately pubescent to nearly glabrous condition of var. *brevipes*.

Descurainia sophia (L.) Webb. [*Sisymbrium sophia* L.; *Sophia sophia* (L.) Britton; *Sophia parviflora* Standl.] Plants annual or infrequently winter annual, stems 1.7-8.5 (10) dm tall or more, simple or more commonly branched above, softly dendritic- or mixed simple- and dendritic-hairy at least below; leaves basal and cauline, 1-12 cm long, the lower 2-3 times pinnately compound to pinnatifid, with 2-6 pairs of pinnatifid pinnae, the upper ones smaller and usually twice pinnately compound or pinnatifid; pedicels 4-17 mm long, ascending, puberulent or glabrous; sepals erect, 2-3.1 mm long, yellowish, glabrous or hairy; petals 2.2-3 mm long, cream; siliques (10) 12-27 (30) mm long, 0.8-1.2 mm wide, ascending-erect; styles 0.1-0.3 mm long; seeds uniseriate, mostly 10-25 mm long.— Roadsides, corrals, agricultural lands, foothills, and other disturbed sites from 750 to 2450 m elevation in Beaver, Emery, Garfield, Grand, Juab, Millard, San Juan, Summit, Uintah, Washington, and Weber counties, and probably cosmopolitan in Utah; widespread in North America; adventive from Europe.

DIPLOTAXIS DC.

Plants glabrous or simple-hirsute annuals or biennials, from taproots; leaves alternate, mostly basal, pinnatifid to irregularly toothed, reduced upwards and petiolate to merely sessile but not auriculate; pedicels ascending or ascending-spreading, not subtended by bracts; sepals 4, deciduous; petals 4, yellow or sometimes fading rose; stamens 6, filaments lacking glandular processes; styles stout, well developed, stigma capitate; fruit a silique, many times longer than broad, linear, somewhat flattened parallel to partition, valves 1-3-nerved, beak not nerved; seeds numerous, biseriate.

A genus of perhaps 20 species of Eurasia.

Diplotaxis muralis (L.) DC. [*Sisymbrium murale* L.] Plants erect or ascending, pubescent with coarse, descending hairs at least below, stems 0.7-5 dm tall, usually branched; basal leaves lyrate-pinnatifid to irregularly lobed, mostly 2.5-9.5 cm long, 0.5-3.5 cm wide; cauline leaves usually much reduced upwards, all petiolate, not auriculate; pedicels 6-23 mm long or more, slender, ascending to spreading-ascending, often hirsute; sepals 3-4.5 mm long, purplish tinged, glabrous or hirsute; petals 4.5-7.5 mm long, yellow or sometimes fading rose;

siliques 17-33 mm long, 1.5-2.8 mm wide; style 1.5-2.5 mm long, valves glabrous, lightly 1-3-nerved.— Fields and disturbed sites in Cache County, and to be expected elsewhere; scattered in North America; adventive from Europe.

DITHYREA Harv.

Plants stellate or dendritic hairy, annuals or winter annuals, from taproots; leaves alternate, simple, subentire to toothed, lobed or pinnatifid, petiolate to sessile but not auriculate; flowers racemose, pedicels spreading, not subtended by bracts; sepals 4, deciduous; petals 4, white; stamens 6, filaments lacking glandular processes; style broad and stout, stigma enlarged-capitate; fruit a silicle, more than twice longer than broad, spectaclelike, compressed at right angles to the replum, valves reticulately veined; seeds 1 per locule.

A genus of 2 species of western North America.

Dithyrea wislizenii Engelm. in Wisliz. Spectacle-pod. Plants erect or ascending, pubescent with soft stellate or dendritic hairs, stems 0.7-5 dm tall, simple or branched; basal leaves often withered by anthesis; cauline leaves 1.2-9.5 cm long, 0.2-2.5 cm wide, pinnatifid, sinuately dentate, irregularly lobed, or entire, moderately to densely hairy like stems, reduced upwards; pedicels 5-21 mm long in fruit, spreading, dendritic hairy; sepals 3-5.5 mm long, greenish, yellowish, or purplish, usually dendritic hairy; petals 4.8-8 mm long, white, claws occasionally lavender, blades orbicular to spatulate, 2.5-5.5 mm wide; silicles 4-6.5 mm long (from apex of the short stipe), 9-14 mm wide, valves pubescent; seeds 1 per locule.— Sandy sites in warm desert shrub, grassland, and pinyon-juniper communities from 750 to 1700 m elevation in Emery, Garfield, Grand, Kane, San Juan, and Washington counties; Colorado, Oklahoma, and Texas westward to Utah and Arizona.

There is much variation in leaf form, but this does not seem to be correlated with other features or with ecological variations.

DRABA L.

Plants with stellate, dendritic, forked, or simple hairs, or glabrate, annual, biennial, or perennial, from taproots and often with well-developed caudices; leaves all basal or some cauline, alternate, simple, entire or toothed, tapering to the base or rounded, not auriculate; flowers racemose, pedicels usually not subtended by bracts; sepals 4, deciduous; petals 4, white, yellow or cream, apex rounded to bifid; stamens 6, filaments lacking glandular processes; style obsolete to prominent and slender, stigma obscurely bilobed; fruit a silicle or infrequently a short silique, mostly 1-10 times longer than broad, ovale to ovate, lanceolate or linear, compressed parallel to septum, plane or twisted, straight or curved, valves obscurely 1-nerved or nerveless; seeds biseriate, usually numerous.

A genus of 250 to 300 species mainly of the northern temperate region of the world.

Hartman, R. L., et al. 1975. Biosystematics of *Draba cuneifolia* and *D. platycarpa* (Cruciferae) with emphasis on volatile and flavonoid constitutents. Brittonia 27:317-327.

Hitchcock, C. L. 1941. A revision of the drabas of western North America. Univ. Wash. Publ. Biol. 11:1-132.

Payson, E. B. 1917. The perennial scapose drabas of North America. Amer. J. Bot. 4:253-267.

1. Plants scapose, leaves all basal, mostly depressed-cespitose perennials (except in *D. verna* which has deeply bilobed petals) .... KEY I.
   Plants with one to many cauline leaves in addition to basal ones, annual (and the petals not bilobed), biennial, or perennial plants .... KEY II.

Key I.
Plants scapose

1. Plants annual, flowering in springtime; style scarcely if at all evident (up to 0.1 mm long) .... *D. verna*

Plants perennial, flowering in springtime and in summer; styles 0.15-2.5 mm long 2

2(1). Petals white 3
Petals yellow 6

3(2). Plants pubescent throughout with doubly pectinate hairs; known only from Daggett County .... *D. oligosperma*
Plants variously hairy, but either stellate or with simple or forked hairs only, seldom or nearly pubescent throughout; known from Uinta and Wasatch mountains and plateaus of southern Utah 4

4(3). Leaves with simple hairs only; petals 2-3 mm long; styles up to 0.2 mm long .... *D. fladnizensis*
Leaves variously pubescent; petals mostly 3-5 mm long; styles 0.2-0.5 mm long 5

5(4). Leaves cinereous with appressed hairs, sometimes stellate; plants of high elevations in Wasatch and Uinta mountains .... *D. lonchocarpa*
Leaves glabrous above and below, ciliate with simple or forked hairs; plants of plateaus of southern Utah .... *D. subalpina*

6(2). Leaves glabrous or with unforked hairs only, often merely ciliate 7
Leaves pubescent, at least some of the hairs forked, stellate, or doubly pectinate 9

7(6). Styles 1-2.5 mm long; petals 5-6 mm long; plants of Box Elder and Weber counties .... *D. maguirei*
Styles usually less than 1 mm long; petals less than 5 mm long; distribution various 8

8(7). Styles not over 0.2 mm long; plants biennial or short-lived perennial, leaves not densely imbricated; petals 1.5-3 mm long .... *D. crassifolia*
Styles 0.2-1 mm long; plants perennial, densely cespitose, with closely imbricated leaves; petals often more than 3 mm long .... *D. densifolia*

9(6). Lower side of leaves (at least) with appressed, pectinately branched hairs; plants of Wasatch and Uinta mountains .... *D. oligosperma*
Lower side of leaves glabrous or pubescent, but, if so, with merely stellate or forked hairs, not pectinate 10

10(9). Leaves almost glabrous, ciliate with forked or dendritic hairs; plants of Box Elder and Weber counties .... *D. maguirei*
Leaves more or less pubescent on one or both surfaces 11

11(10). Stems glabrous, at least above 12
Stems pubescent throughout 13

12(11). Basal leaves 1-3.5 cm long, 0.3-1 cm wide; silicles 7-14 mm long, 2-4 mm wide; plants of Washington County .... *D. asprella*
Basal leaves 0.6-1.2 cm long, 0.9-1.4 cm wide; siliques 4-10 mm long, 1.5-3 mm wide; plants of Cache County .... *D. maguirei*

13(11). Leaves densely cinereous pubescent, individual hairs almost indistinguishable; known from Uinta Mountains .... *D. ventosa*
Leaves not densely cinerous pubescent, individual hairs apparent; plants of Garfield and Piute counties .... *D. sobolifera*

Key II.
Plants with 1 or more cauline leaves

1. Plants annual; styles obsolete or rarely up to 0.2 mm long 2
Plants biennial or perennial; styles mostly 0.2-1 mm long or more 7

2(1). Upper portion of stem, including pedicels, pubescent 3
Upper portion of stem glabrous 4

3(2). Flowers white; plants widely distributed at low elevations .... *D. cuneifolia*
Flowers yellow; plants of montane regions in northern Utah .... *D. rectifructa*

4(2). Upper leaf surfaces usually glabrous; cauline leaves 1 or 2, rarely lacking .... *D. crassifolia*
Upper leaf surfaces usually pubescent; cauline leaves 1-5 or more 5

5(4). Petals white; leaves entire or nearly so; silicles less than 2 mm wide; plants of low elevations .... *D. reptans*
Petals yellow, sometimes fading whitish; silicles at least 2 mm wide or the plants of montane places 6

6(5). Pedicels usually at least 1.5 times longer than the silicles; plants usually of low elevations .... *D. nemorosa*
Pedicels rarely up to 1.5 times longer than the silicles; plants usually of montane places .... *D. stenoloba*

7(1). Petals white; plants of high elevations 8
Petals yellow or cream, sometimes fading whitish; plants of low to moderate or high elevations 10

8(7). Styles obsolete or nearly so, less than 0.2 mm long .... *D. fladnizensis*
Styles 0.2-0.8 mm long 9

9(8). Silicles glabrous or merely ciliate; cauline leaves 1 or 2 .... *D. lonchocarpa*
Silicles pubescent on valves; cauline leaves 1-10 .... *D. lanceolata*

10(7). Cauline leaves solitary; plants of low elevations, restricted to Washington County .... *D. asprella*
Cauline leaves usually 2-20, or if solitary then not of Washington County; plants not or rarely of Washington County 11

11(10). Styles obsolete or nearly so, up to 0.2 mm long .... *D. stenoloba*
Styles 0.2-2.5 mm long 12

12(11). Petals 2.8-3.8 mm long; pubescence of leaves stiff, stalked, 2—5-rayed hairs; silicles pubescent with simple or stalked and forked hairs .... *D. brachystylis*
Petals (3.8) 4-8 mm long; pubescence of leaves various; silicles glabrous or pubescent with stellate to simple hairs 13

13(12). Leaf surfaces glabrous, ciliate or margins smooth; silicles glabrous .... *D. crassa*
Leaf surfaces with stalked 2—4-rayed, forked, or simple hairs, margins ciliate or not; silicles glabrous or hairy 14

14(13). Leaves solitary, subtending lowermost flower or branch of inflorescence; plants of Box Elder County .... *D. incerta*
Leaves 2-20; plants of various distribution 15

15(14). Leaves bright green to somewhat grayish; cauline leaves often denticulate;

silicles plane or slightly contorted; plants of Grand and San Juan counties .... *D. spectabilis*

Leaves grayish-green; cauline leaves entire; silicles usually contorted; plants of broad distribution .... *D. aurea*

Draba asprella Greene. Plants perennial, cespitose, stems 0.5-1.4 (2) dm tall, arising from a branching caudex, hirsute with mixed simple and forked to dendritic hairs; leaves all basal, rarely with one cauline, 1-3.5 cm long, 0.3-1 cm wide, oblanceolate to spatulate, entire or obscurely denticulate, green, surfaces more or less pubescent with usually stalked and 4-rayed hairs; racemes simple, 10—30-flowered, elongating in fruit; pedicels 3-15 mm long, ascending, glabrous; sepals 1.8-2.5 mm long, greenish, stellate-hairy; petals 3.4-5 (6) mm long, yellow to yellow-orange, obovate-spatulate, rounded; silicles 7-14 mm long, 1.5-4 mm wide, lance-elliptic, glabrous or ciliate; styles 0.8-1.1 mm long; seeds 12-20.— Talus slopes and low hills from 1050 to 1700 m elevation in Zion Canyon and south of St. George (*Higgins s.n.*, 12 Apr 1961; DIX), Washington County; Arizona. Our material belongs to var. *zionensis* (C. L. Hitchc.) Welsh & Reveal, stat. & comb. nov., based on *Draba zionensis* C. L. Hitchc., Univ. Wash. Publ. Biol. 11:49. 1941. The var. *asprella* is restricted to Arizona.

Draba aurea Vahl in Hornem. [*D. luteola* Greene; *D. surculifera* A. Nels.; *D. aureiformis* Rydb.; *D. uber* A. Nels.; *D. mccallae* Rydb.; *D. decumbens* Rydb.; *D. aurea* var. *luteola* (Greene) O. E. Schulz; *D. aurea* var. *aureiformis* (Rydb.) O. E. Schulz; *D. aurea* var. *decumbens* (Rydb.) O. E. Schulz; *D. aureiformis* var. *leiocarpa* Payson & St. John] Plants perennial, not cespitose, stems 0.7-4 (5) dm tall, simple or few from a branching caudex, pubescent throughout with simple hairs often intermixed with forked ones; basal leaves 0.8-4 cm long, 0.2-1.3 cm wide, oblanceolate, entire or serrulate, green or grayish, surfaces pubescent with stalked 4-rayed hairs; cauline leaves mostly 3-20, lanceolate to ovate or oblanceolate, 0.5-3 cm long, 0.3-1.2 cm wide, entire or less commonly denticulate, pubescent like the basal ones; racemes simple or branched, several- to many-flowered, much elongating in fruit; pedicels 3-15 (20) mm long, ascending to erect, pubescent; sepals 2-3.5 mm long, greenish, pubescent; petals (3.5) 4-6 mm long, yellow, spatulate to obovate, rounded to emarginate; silicles 8-17 mm long, plane or more commonly contorted, 2-4 mm wide, ovate-lanceolate to lanceolate or elliptic, pubescent with simple, branched, or stellate hairs; styles (0.3) 0.8-1.3 (1.5) mm long; seeds 20-50.— Woodlands, grasslands, and among shrubs from 2300 to 3800 m elevation in Beaver, Carbon, Daggett, Duchesne, Garfield, Piute, Salt Lake, San Juan, Sevier, Summit, Uintah, and Utah counties; Alaska and Yukon east to Labrador and Greenland, south to Arizona and New Mexico. This is a highly variable taxon in our region.

Draba brachystylis Rydb. Plants (annual) biennial or short-lived perennial, not cespitose, stems (1) 1.3-2.5 (3) dm tall, usually branched, pubescent throughout with simple, branched, or stellate hairs; basal leaves 1-5.3 cm long, 0.3-1.5 cm wide, oblanceolate, entire or denticulate, surfaces pubescent with stalked 2—5-rayed hairs; cauline leaves (1) 2-8, ovate to obovate, elliptic, or lanceolate, 0.6-2.8 cm long, 0.2-1.1 cm wide, denticulate to entire, pubescent like the basal ones; racemes simple or branched, several- to many-flowered, elongating in fruit; pedicles 1-10 mm long, spreading to spreading-ascending, pubescent; sepals 2-2.7 mm long, yellowish, pubescent; petals 2.8-3.8 mm long, yellow, spatulate, rounded to emarginate; silicles (7) 10-15 mm long, 2-3.5 mm wide, plane, obliquely oblong-elliptic, pubescent with simple and branched hairs; styles 0.4-0.8 mm long; seeds 20-30.— Woodlands and shrublands from 1675 to 2130 m elevation in Salt Lake and Utah counties; Spring Mountains, Clark County, Nevada. This is a poorly known and rarely collected plant with affinities to both *D. aurea* and *D. rectifructa*. The type is from the Wasatch Mountains.

Draba crassa Rydb. [*D. chrysantha* var. *crassa* (Rydb.) O. E. Schulz] Plants perennial, not cespitose, stems 0.8-1.8 dm tall, arising from a thickened caudex clothed with numerous marcescent leaf-bases, moderately hairy with simple or branched hairs, at least below; basal leaves 1.5-8 cm long, 0.3-1.2 cm wide, elliptic to oblanceolate, entire or obscurely toothed, glabrous or merely ciliate; cauline leaves 2-8, ovate to elliptic or obovate, 0.5-2 cm long, 0.2-0.8 cm wide, entire or nearly so, usually glabrous; racemes few- to many-flowered, elongating in fruit; pedicles 3-10 mm long, ascending, softly villous; sepals 2.3-3 mm long, greenish, suffused with purple, pubescent; petals 4-8 mm long, yellow, obovate, rounded; silicles 8-15 mm long, 2.5-4 (5) mm wide, plane or contorted, ovate to lanceolate or elliptic, glabrous; styles 0.8-1.2 mm long; seeds 14-26.— Alpine tundra from 3500 to 3800 m elevation in the Uinta Mountains of Summit County but to be expected in Daggett, Duchesne, and Uintah counties; Montana, Wyoming, and Colorado.

Draba crassifolia R. Graham. [*D. parryi* Rydb.; *D. crassifolia* var. *parryi* (Rydb.) O. E. Schulz] Plants (annual) biennial or short-lived perennial, not cespitose, stems 0.2-1.2 (2) dm tall, arising from a resulate tuft of leaves, usually glabrous except for a few hairs near base; basal leaves 0.3-1.5 (2.3) cm long, 0.1-0.3 cm wide, narrowly spatulate, entire, surfaces usually glabrous, sometimes ciliate; cauline leaves lacking or 1 or 2, very small; racemes 2- to several-flowered, congested or elongating in fruit; pedicels 2-10 mm long, curved-ascending, glabrous; sepals 1-1.4 mm long, greenish, glabrous; petals 1.7-2.5 mm long, yellow but rarely fading white, elliptic-spatulate, emarginate; silicles 5-10 mm long, 1.5-2.5 mm wide, plane, glabrous, lance-elliptic; styles up to 0.5 mm long; seeds 10-60.— Alpine tundra from 3050 to 3800 m elevation in Duchesne (US), Grand, Piute, Salt Lake, San Juan, Sanpete (US), Sevier, and Summit counties; widespread from Alaska and Yukon east to Greenland and south to California, Arizona, and Colorado; Europe. This entity apparently grades with some phases of *D. stenoloba* in Utah, from which it is difficult, if not impossible, to segregate all specimens.

Draba cuneifolia Nutt. ex Torr. & Gray. Plants annual, not cespitose, 0.1-1.5 (2) dm tall, very short leafy stems arising from a taproot, simple or branched, more or less dendritic-hairy throughout; basal leaves 0.5-4 cm long, 0.2-2.7 cm wide, suborbicular to oblanceolate or cuneate-spatulate, dentate to entire, surfaces hirsute with stalked 2—4-rayed hairs, sometimes intermixed with simple hairs; cauline leaves few to several, usually much reduced, pubescent like the basal ones; racemes 3- to many-flowered, congested or elongating in fruit; pedicels 1-7 mm long, spreading to ascending, dendritic-hairy; sepals 1.5-2.5 mm long, greenish, pubescent; petals 3-4.5 (5) mm long, occasionally small or even lacking in cleistogamous flowers, white, spatulate, rounded to emarginate; silicles 4-13 (15) mm long, 1.8-3.8 (5) mm wide, plane, strigose, oblong-elliptic; styles up to 0.2 mm long; seeds 20 or more.— Warm desert shrublands upwards to mountain brush, pinyon-juniper, and ponderosa pine communities, from 750 to 2300 m elevation in much of Utah; Washington and Idaho south to Mexico, Texas, and Arkansas. Two varieties are present.

1. Racemes compact in fruit, seldom half as long as plant height .... *D. cuneifolia* var. *cuneifolia*

   Racemes much elongated in fruit, commonly at least half plant height .... *D. cuneifolia* var. *platycarpa*

Var. ***cuneifolia.*** [*D. helleri* Small; *D. ammophila* Heller; *D. cuneifolia* var. *helleri* (Small) O. E. Schulz; *D. cuneifolia* var. *leiocarpa* O. E. Schulz] This is our common variant, being in Beaver, Box Elder, Grand, Kane, Millard, San Juan, Sevier, Uintah, Utah, and Washington counties; Colorado west to California and south to Mexico and Texas.

Var. ***platycarpa*** (Torr. & Gray) S. Wats.

[*D. platycarpa* Torr. & Gray; *D. viperensis* St. John] Our few specimens from Washington County are tentatively assigned to this taxon, but they differ *inter alia* in having longer and narrower silicles; Arkansas westward to California, north to Washington.

Draba densifolia Nutt. ex Torr. & Gray. Plants perennial, pulvinate-cespitose and matted, scapose, arising from compacted caudex branches clothed with marcescent leaf-bases, scapes 0.5-1.5 dm tall, glabrous to pubescent throughout; leaves 0.2-0.9 cm long, mostly 0.1-0.3 cm wide, oblong to oblanceolate, surfaces glabrous or with few-forked or dendritic hairs beneath, more or less ciliated with stiff, coarse, simple or forked hairs; racemes 2- to 10 (or more)-flowered, not elongated in fruit; pedicels 0.5-2 mm long, ascending, glabrous; sepals 2-3 mm long, greenish, glabrous or pubescent; petals 2-6 mm long, yellow, obovate, truncate to emarginate; silicles 2-7 mm long, 2-3.5 mm wide, ovate to elliptic, glabrous; styles 0.2-1 mm long; seeds 2-12.— Alpine tundra from 3050 to 3800 m elevation of Wasatch and Uinta mountains in Daggett, Duchesne, Salt Lake, Summit, and Uintah counties; British Columbia and Montana south to California, Nevada, Utah, and Wyoming. Two weakly defined, sympatric variants are recognized.

1. Styles 0.2-0.5 mm long; plants glabrous except for cilia of the leaves .... *D. densifolia* var. *daviesiae*
   Styles 0.5-1 mm long; plants sometimes hairy on the lower leaf surfaces and on the scape .... *D. densifolia* var. *densifolia*

Var. ***daviesiae*** (C. L. Hitchc.) Welsh & Reveal, comb. nov., based on *Draba apiculata* var. *daviesiae* C. L. Hitchc., Univ. Wash. Publ. Bot. 17(2):489. 1964. [*D. apiculata* C. L. Hitchc.] This is a poorly differentiated phase of alpine sites in Duchesne, Salt Lake, Summit, and Uintah counties; Wyoming, Montana. The type of *D. apiculata* is from LaMotte Peak, Uinta Mountains, Utah.

Var. ***densifolia***. [*D. glacialis* var. *pectinata* S. Wats.; *D. mulfordae* Payson; *D. nelsonii* Macbride & Payson; *D. globosa* Payson; *D. sphaerula* Macbride & Payson; *D. pectinata* (S. Wats.) Rydb.; *D. caeruleomontana* Payson & St. John; *D. caeruleomontana* var. *piperi* Payson & St. John; *D. densifolia* f. *nelsonii* (Macbride & Payson) O. E. Schulz; *D. globosa* var. *sphaerula* (Macbride & Payson) O. E. Schulz] This is the common phase of the species in alpine sites of Daggett, Duchesne, Salt Lake, Summit, and Uintah counties; distribution of the species.

Draba fladnizensis Wulfen in Jacq. [*D. pattersonii* O. E. Schulz; *D. pattersonii* var. *hirticaulis* O. E. Schulz; *D. pattersonii* var. *dasycarpa* O. E. Schulz] Plants perennial, not cespitose, stems 0.2-0.9 dm tall, glabrous or pubescent at least near the base with simple or forked hairs; basal leaves 0.3-1 cm long, 0.1-0.2 cm wide, oblanceolate, surfaces glabrous or moderately hairy with 1—2-forked hairs, cilitate; cauline leaves 1 or 2, greatly reduced; racemes 3-to several-flowered; pedicels 1-3 mm long, ascending to spreading, glabrous; sepals 1.2-1.8 mm long, greenish, glabrous; petals 1.8-2.5 mm long, white (rarely pink), spatulate, rounded to retuse; silicles 3-6 mm long, 1.2-2 mm wide, oblong-ovate, glabrous; styles essentially lacking; seeds 10-20.— Alpine tundra in Uinta and La Sal mountains above 3100 m elevation in Daggett (?), Grand, San Juan, and Uintah (?) counties; Alaska to Mackenzie south to Colorado and Utah. Our material is difficult to interpret from the dwarf alpine specimens of *D. stenoloba* (q.v.), but apparently the white petals are diagnostic.

Draba incerta Payson. [*D. laevicapsula* Payson; *D. incerta* var. *laevicapsula* (Payson) Payson & St. John] Perennial, cespitose but loosely so, 0.2-1.5 (2) dm tall, stems pubescent with stellate or dendritic and sometimes simple hairs; basal leaves 0.5-1.8 (2.5) cm long, 0.1-0.3 cm wide, narrowly oblanceolate, surfaces with at least some doubly pectinate hairs, often intermixed with other types of pubescence, margin ciliate with simple to pectinately branched hairs; cauline leaves 1 or lacking; racemes 5- to many-flowered, elongating in fruit; pedicels 2-12 mm long, ascending, usually hairy; sepals 2.5-3.5 mm long, greenish or suffused with purple, pubescent; petals 4-5.5 mm long, yellow but fading cream, cuneate-obovate, broadly emarginate; silicles 6-10 mm long, 2.5-3.5 mm wide, ovate to lanceolate, plane, pubescent or glabrous; seeds 8-14.— Alpine sites above 3050 m elevation in Raft River Mountains of Box Elder County; Alaska and Yukon south to Washington, Utah, and Wyoming.

Draba lanceolata Royle. [*D. cana* Rydb.; *D. valida* Goodding] Plants perennial, loosely cespitose, caudex simple or branched, stems 0.5-3.5 dm tall, pubescent throughout with soft many-branched hairs; basal leaves 0.5-4 cm long, 0.1-0.4 cm wide, oblanceolate, entire, pubescent of overlapping, stellate or branched hairs; cauline leaves several, commonly toothed; racemes several- to many-flowered, sometimes with solitary flowers in upper leaf axils; pedicels 2-9 mm long, erect, usually appressed to rachis, pubescent; sepals 1.5-2 mm long, sparsely pilose; petals 2.2-4 mm long, white, cuneate-obovate, more or less emarginate; silicles 5-12 mm long, 1.5-2.5 mm wide, narrowly lanceolate to oblong, plane or contorted, softly pubescent, rarely glabrous; styles 0.2-0.8 mm long; seeds 20 or more.- Alpine meadows and krumholz in the Uinta and Henry mountains mostly above 3000 m elevation, in Daggett, Duchesne, Garfield, Summit, and Uintah counties; Alaska and Yukon south to Nevada, Utah, and Colorado. The type of *D. valida* is from Dyer Mine, Uintah County.

Draba lonchocarpa Rydb. Plants perennial, loosely to densely cespitose, caudex usually branched, scapose or rarely with one cauline leaf, scape 0.1-1.2 dm tall, glabrous or pubescent with soft many-branched hairs; leaves 0.5-1.5 cm long, 0.1-0.4 cm wide, pubescent with usually overlapping or stellate, rarely some simple, hairs, marginal pubescence entirely stellate or with some simple hairs; racemes 3—12-flowered, contracted or elongating in fruit; pedicels 1-6 (11) mm long, ascending to erect, glabrous; sepals 1.5-2 mm long, glabrous or pubescent; petals 2.5-4 mm long, white; silicles 5-14 mm long, 1-2 mm wide, linear to lance-linear or oblong, plane or twisted, glabrous or pubescent; styles 0.2-0.5 mm long; seeds 8-30.— Alpine tundra in Wasatch and Uinta mountains; Alaska and Yukon south to Oregon, Utah, and Colorado. Our material has been treated as portions of an expanded *D. nivalis* Lilj., from which it differs in technical features of pubescence and silicle characteristics. Two sympatric variants have been designated among the Utah material.

1. Silicles mostly less than 7 mm long, elliptic to linear .... *D. lonchocarpa* var. *exigua*
   Silicles mostly more than 10 mm long, linear to narrowly elliptic .... *D. lonchocarpa* var. *lonchocarpa*

Var. *exigua* O. E. Schulz. [*D. nivalis* var. *exigua* (O. E. Schulz) C. L. Hitchc.] Alpine tundra in Uinta and La Sal mountains of Duchesne, Grand, and Summit counties; Wyoming and Colorado.

Var. *lonchocarpa*. [*D. nivalis* var. *elongata* S. Wats.; *D. lonchocarpa* var. *dasycarpa* O. E. Schulz; *D. lonchocarpa* var. *vestita* O. E. Schulz; *D. lonchocarpa* var. *semitonsa* St. John] Alpine sites from 3050 to 3900 m elevation in the Wasatch, Uinta, and La Sal mountains of Cache, Duchesne, Grand, Salt Lake, San Juan, and Summit counties; Alaska south to Oregon, Utah, and Wyoming.

Draba maguirei C. L. Hitchc. Plants perennial, cespitose, with substoloniferous branches, scapose, scapes 0.2-2 dm tall, glabrous or with a few forked hairs near base; leaves 0.3-1.5 cm long, 0.1-0.4 cm wide, oblong-oblanceolate to obovate-oblanceolate, surfaces glabrous or nearly so, ciliate with simple, forked, or 4-rayed, shortly stalked hairs; racemes few- to several-flowered, elongating in fruit; pedicels 2-10 (15) mm long, ascending, glabrous; sepals 2-3 mm long, yellowish, glabrous; petals 4.5-6 mm long, yellowish, spatulate, rounded; silicles 4-9 mm long, 2-3.5 mm wide, ovate to lanceolate, oblique, glabrous or scaberulous; styles 1-1.5 mm long; seeds 2-8.— Talus slopes and rocky outcrops from 2600 to 2900 m elevation in northern Utah. Two tenuous and somewhat arbitrary varieties have been designated.

1. Hairs of leaves all simple or rarely some forked .... *D. maguirei* var. *burkeri*
   Hairs of leaves all branched, mostly 4-rayed .... *D. maguirei* var. *maguirei*

Var. ***burkeri*** C. L. Hitchc. Cottonwood Canyon, Wellesville Mountains, Box Elder County (type locality), and mountains east of Ogden, Weber County; endemic.

Var. ***maguirei.*** Apparently restricted to the Bear River Range, Cache County (type from Mt. Naomi); endemic.

Draba nemorosa L. [*D. dictyota* Greene] Annual, from a slender taproot, stems simple or branched, 0.5-2.5 dm tall, pubescent with mixed forked and stellate hairs, or less commonly with some simple ones, or even glabrate; leaves 0.3-3 cm long, 0.2-0.8 cm wide, oblanceolate to lanceolate, ovate or oblong, entire or toothed, pubescent with branched or simple hairs; racemes few- to many-flowered, much elongating in fruit; pedicels 5-25 mm long, spreading-ascending, glabrous; sepals 1-1.5 mm long, green to yellowish or suffused purple, pilose to glabrous; petals 1.2-4 mm long, yellow to white; silicles 4-10 mm long, 1.5-3 mm wide, oblong to oblanceolate or elliptic, plane, glabrous; styles obsolete; seeds 25 or more.— Roadsides, foothills, and dry exposed sites from 1375 to 2250 m elevation in Box Elder, Cache, Salt Lake, Summit, Uintah, Utah, Weber, and perhaps all other counties; common throughout much of North America and Eurasia.

Draba oligosperma Hook. Perennial, cespitose, the caudex much branched, scapose, the scapes 0.1-1 dm tall, pubescent throughout with pectinate or stellate hairs or glabrous, at least below; leaves 0.3-1.2 cm long, 0.1-0.2 cm wide, linear to spatulate or oblong, surfaces (one or both) pubescent with sessile, appressed, doubly pectinate-branched hairs, commonly ciliate with at least some pectinately branched hairs; racemes 2—15-flowered, only moderately elongating in fruit; pedicels 1-10 mm long, ascending, glabrous or pubescent; sepals 1.5-2.5 mm long, yellowish, pubescent; petals 3-5 mm long, yellow or white, obovate, rounded to emarginate; silicles 3-8 mm long, 2-4 mm wide, ovate to oval or oblong, plane, glabrous to pubescent; styles 0.1-1.2 mm long; seeds 2-10.— Ponderosa pine and Douglas fir woodlands upwards to alpine tundra in the Wasatch and Uinta Mountains from 2290 to 3800 m elevation; British Columbia and Alberta south to California, Utah, and Wyoming. Two varieties are known.

1. Petals yellow; pubescence of silicles, when present, of simple or forked hairs only; plants widespread .... *D. oligosperma* var. *oligosperma*
   Petals evidently white; pubescence of silicles at least in part of doubly pectinate hairs; plants of Daggett County .... *D. oligosperma* var. *pectinipila*

Var. ***oligosperma.*** [*D. oligosperma* var. *andina* (Nutt.) ex Torr. & Gray: *D. andina* (Nutt.) A. Nels.; *D. saximontana* A. Nels.; *D. oligosperma* var. *microcarpa* Blankinship; *D. oligosperma* var. *saximontana* (A. Nels.) O. E. Schulz; *D. oligosperma* var. *leiocarpa* O. E. Schulz. Widespread in the Wasatch and Uinta mountains in Cache, Daggett, Duchesne, Summit, Uintah, and Utah counties; range of the species.

Var. ***pectinipila*** (Rollins) C. L. Hitchc. [*D. pectinipila* Rollins] Vicinity of Flaming Gorge, Daggett County, where possibly extirpated; Wyoming.

Draba rectifructa C. L. Hitchc. [*D. montana* S. Wats., not Bergeret] Annual, from a slender taproot, stems simple or branched, 1-2.2 dm tall, pubescent throughout although sparsely so above in some with branched and/or simple hairs; leaves 0.5-3 cm long, 0.1-0.7 cm wide, lanceolate to oblanceolate, entire, pubescent with branched and simple hairs intermixed; racemes several- to many-flowered, much elongating in fruit; pedicels 2-6 mm long, spreading to curved-ascending, pubescent; sepals 1.2-1.7 mm long, greenish, pubescent; petals 2-4 mm long, yellow, narrowly spatulate, usually emarginate; silicles (4) 6-10 mm long, 2-2.5 mm wide, obliquely oblong, pubescent; styles obsolete; seeds 40 or more.— Roadsides, foothills, meadows, and woodlands, mostly from 2200 to 3050 m elevation in Carbon, Duchesne, Garfield, Grand, Piute, Salt Lake, and Wasatch counties (and to be expected elsewhere); Colorado, New Mexico, and Arizona.

Draba reptans (Lam.) Fern. Annual, from a slender taproot, 0.2-1 (2) dm tall, very short leafy stem simple or sometimes branched, pubescent with simple to stellate hairs below, glabrous above; basal leaves 0.3-1.8 cm long, 0.1-1 cm wide, spatulate to ovate or obovate, usually entire, surfaces pubescent with branched or forked hairs or upper surface only of simple hairs; cauline leaves few, usually reduced, pubescent like basal ones, or upper surface with simple hairs; racemes (1-) several- to many-flowered, compact in fruit; pedicels 1-6 mm long, ascending, glabrous; sepals 1.5-2.5 mm long, greenish or yellowish, usually pubescent; petals 3-5 mm long, white, ovate, rounded, sometimes smaller or lacking in cleistogamous flowers; silicles 5-20 mm long, 1-2 mm wide, oblong, nearly erect, pubescent or glabrous; styles up to 0.15 mm long; seeds 15 or more.— Dry exposed sites from 1200 to 2000 m elevation in the northern two-thirds of Utah (but possibly cosmopolitan); throughout much of northern North America. Two more or less arbitrary varieties are present. *Draba reptans* is similar to, and not always distinct from, *D. cuneifolia* (q.v.).

1. Upper surface of the cauline leaves and one or both surfaces of the basal leaves pubescent with mostly simple hairs .... *D. reptans* var. *reptans*
   Upper surface of all leaves predominantly pubescent with forked or branched hairs .... *D. reptans* var. *stellifera*

Var. *reptans*. [*Arabis reptans* Lam.; *D. caroliniana* Walter; *D. micrantha* Nutt. ex Torr. & Gray; *D. coloradoensis* Rydb.; *D. reptans* var. *micrantha* (Nutt.) Fern.] Range of the species.

Var. *stellifera* (O. E. Schulz) C. L. Hitchc. [*D. carolinana* f. *stellifera* O. E. Schulz; *D. carolinana* ssp. *stellifera* (O. E. Schulz) Payson & St. John] Sympatric with the former.

Draba sobolifera Rydb. [*D. uncinalis* Rydb.; *D. sobolifera* var. *uncinalis* (Rydb.) O. E. Schulz] Perennial, cespitose, caudex branched, scapose, scapes 0.1-0.6 dm tall, pubescent with intermixed stellate, branched, and simple hairs; leaves 0.8-2 cm long, 0.2-0.5 cm wide, obovate to oblanceolate, pubescent with stalked stellate or 4-rayed hairs at least beneath, and usually ciliate with simple hairs at base; racemes (2-) 5—20-flowered, compact to elongating in fruit; pedicels 3-8 mm long, stellate or with branched hairs; sepals 1.8-2.5 mm long; petals 4-5 mm long, yellow, obovate; silicles 3-8 mm long, 2.5-4 mm wide, ovate to elliptic, pubescent to glabrous; styles 0.4-1 mm long; seeds 4-12.— Sagebrush communities upwards to alpine tundra, from 2290 to 3660 m elevation in Tushar Mountains and on Markagaunt Plateau in Beaver, Garfield, and Piute counties; endemic.

The types of both *Draba sobolifera* and *D. uncinalis* were collected by Marcus E. Jones in the Delano Peak area west of Marysvale, Piute County.

Draba spectabilis Greene. [*D. spectabilis* var. *glabrescens* O. E. Schulz] Perennial, not cespitose, caudex branched, stems mostly 1-4 dm tall, usually simple, pubescent with simple or forked hairs; basal leaves (0.5) 1-4 cm long, 0.2-1 cm wide, obovate to spatulate, subentire to denticulate, green, surfaces with subsessile 4-rayed or forked hairs, infrequently with the upper surface glabrous; cauline leaves mostly 3-15, ovate to lanceolate, subentire to sharply toothed, 0.5-2 cm long, 0.2-1.5 cm wide, pubescent like basal ones; racemes several- to many-flowered, much elongating in fruit; pedicels 5-15 mm long or more, ascending, glabrous or hairy; sepals 2-3.5 mm long, yellowish, pubescent; petals 4.5-7 mm long, yellow but fading white, elliptic, rounded; silicles 5-14 mm long, 2-3 mm wide, lanceolate to ovate, plane, glabrous or pubescent; styles 0.8-2.5 mm long; seeds 10-20.— Opening in woods, at moderate to high elevations in La Sal and Abajo mountains of Grand and San Juan counties; Colorado, New Mexico, Arizona. Our material is var. *spectabilis*. The type of var. *glabrescens* was obtained in the La Sal Mountains.

Draba stenoloba Ledeb. [*D. nemorosa* var. *stenoloba* (Ledeb.) M. E. Jones; *D. nitida* Greene; *D. deflexa* Greene; *D. nitida* var. *nana* O. E. Schulz; *D. nitida* var. *praelonga* O. E. Schulz] Plants (annual?) biennial or short-lived perennial, from a taproot, caudex more or less developed, stems 0.3-2.5 dm tall, glabrous or sometimes hirsute below; basal leaves 0.3-4 cm long, 0.2-0.8 cm wide, entire to denticulate, pubescent with simple to forked or branched hairs, or with one or both surfaces glabrous on some leaves; cauline leaves (0) 1-8, ovate to lanceolate or elliptic, entire or denticulate, similar to the basal ones in all respects; racemes several- to many-flowered, elongating in fruit; pedicels 1-14 mm long, ascending, glabrous; sepals 1-2.2 mm long, greenish, glabrous; petals 2-4.5 mm long, yellow to cream or fading white, spatulate, rounded to emarginate; silicles 6-18 mm long, 1.5-2.2 mm wide, linear to oblong or elliptic, usually glabrous; styles up to 0.2 mm long; seeds 16 or more.— Woods, meadows, sagebrush communities and along stream banks from 2075 to 3350 m elevation in Beaver, Box Elder, Cache, Daggett, Duchesne, Emery, Garfield, Piute, Salt Lake, Sevier, Summit, Uintah, Utah, Wasatch, and Washington counties; Alaska and Yukon south to California, Nevada, Utah, and Colorado.

Draba subalpina Goodman & Hitchc. [*D. oriebata* of Utah references, not Macbride & Payson] Perennial, cespitose, caudex simple or branched, clothed with marcescent leaves, scapose, scapes 0.1-1.2 dm tall, rarely with one cauline leaf, glabrous throughout or pubescent with simple or forked hairs at least near base; leaves 0.3-1.8 cm long, 0.1-0.4 cm wide, oblong to spatulate, surfaces glabrous or sparingly hirsute, ciliate with coarse simple or less commonly forked or branched hairs; racemes few- to many-flowered, only moderately elongating in fruit; pedicels (1) 2-10 mm long, usually purplish, glabrous; petals 4-5 mm long, white, cuneate-spatulate, emarginate; silicles 3-8 mm long, 2-4 mm wide, ovate to elliptic, plane or more or less contorted, glabrous; styles 0.6-1 mm long; seeds 6-12.—Spruce-fir, Douglas fir, or bristlecone pine woodlands mostly on the Pink Limestone member of the Wasatch Formation, from 2130 to 3050 m elevation in Garfield, Iron, and Kane counties; endemic.

The type is from Cedar Breaks, Iron County.

Draba ventosa A. Gray. Perennial, cespitose, the caudex usually branched, more or less clothed with marcescent leaves, scapose, scapes 0.2-0.4 dm tall, pubescent with simple and forked or sometimes stellate hairs; leaves 0.5-1.2 cm long, 0.2-0.4 cm wide, elliptic to lanceolate, surfaces pubescent with simple, forked, or branched to stellate hairs; racemes 3- to many-flowered, little elongating in fruit; pedicels mostly 4-8 mm long, ascending, densely pilose to stellate; sepals 2-2.5 mm long, greenish or yellowish, pilose; petals 4-5 mm long, yellow, obovate; silicles 5-8 mm long, 3.5-5.5 mm wide, oval to ovate, plane, densely hairy; styles 0.6-1.2 mm long; seeds 10-16.— Alpine tundra from 3050 to 3800 m elevation in the Uinta Mountains, in Summit (and perhaps elsewhere) County; Wyoming.

This species is poorly known and is seldom collected. Our description is tentative at best, being drawn on only limited material. The Utah plants are supposedly assignable to var. *ventosa*.

Draba verna L. Diminutive annual from a slender taproot, scapose, scapes 0.2-0.5 (1.2) dm tall, glabrous throughout or pubescent near base only; leaves 0.1-1 (2) cm long, 0.08-0.3 cm wide, spatulate to oblanceolate, entire or toothed, pubescent with branched hairs; racemes few- to many-flowered, elongating in fruit; pedicels 2-12 mm long, ascending, glabrous; sepals 0.6-1.1 mm long, greenish or tinged purplish, glabrous or pubescent; petals 1.5-2.5 mm long, white, deeply bilobed; silicles 2-10 mm long, 1-4 mm wide, elliptic to obovate, glabrous; styles up to 0.2 mm long.— Dry open sites from 1375 to 1680 m elevation in Salt Lake and Weber counties; widespread in North America; Asia.

Our material is scanty and cannot be segregated into the two variants reported for North America.

ERYSIMUM L.

Plants pubescent with 2-3 (4)-rayed hairs, annual to perennial, from taproots; leaves alternate or basal and still alternate, simple, entire to toothed, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow to orange pr burnt-orange to purple; stamens 6, filaments lacking glandular processes; style prominent, short to elongate, stigma bilobed; fruit a silique, many times longer than broad, compressed parallel to partition or subterete, valves 1- to several-nerved; seeds uniseriate, many per locule.

A genus of 100 species, mainly of Europe.

Rossbach, G. B. 1958. The genus *Erysimum* (Cruciferae) in North America north of Mexico—A key to species and varieties. Madroño 14:261-267.

1. Petals (10) 12-20 mm long or more; styles mostly 1.5-3 mm long; plants biennial or perennial; widespread in indigenous plant communities .... *E. asperum*
   Petals 3.5-11 mm long; styles usually less than 1.5 mm long (longer in *E. repandum*); plants annual or biennial to short-lived perennial; restricted and weedy or less commonly in indigenous plant communities 2

2(1). Petals 3.5-5 mm long; siliques 12-27 mm long; plants uncommon, annual weeds of moist sites .... *E. chieranthoides*
   Petals mostly 5-11 mm long; siliques (15) 25-100 mm long; plants common, annual, biennial or perennial, of various habitats 3

3(2). Pedicels usually more than 5 mm long, more slender than fruit; siliques ascending to erect, less than 50 mm long; plants indigenous biennial or short-lived perennial .... *E. inconspicuum*
   Pedicels 2-5 mm long, almost or quite as thick as fruit; siliques spreading to curved-ascending, at least some often more than 50 mm long; plants adventive, annual weeds .... *E. repandum*

Erysimum asperum (Nutt.) DC. Wallflower. Biennial or short-lived perennial, with simple or less commonly branched caudex, stems 1.2-8.5 (10) dm tall or more; basal leaves 2-10 (12) cm long, 0.2-1.4 cm wide, sublinear to elliptic or spatulate, entire or denticulate, grayish to green, pubescent with malpighian or Y-shaped appressed hairs; cauline leaves 1.1-10.4 cm long, 0.1-1.5 cm wide, much reduced to little if at all reduced upwards, variously shaped, entire or toothed, pubescent like basal ones; racemes much elongating in fruit; pedicels 3-17 mm long, spreading-ascending to ascending, usually more slender than the fruit; sepals 7.5-14 mm long, yellowish or purplish; petals 12-28 mm long, yellow to yellow-orange or burnt-orange; siliques (17) 20-115 mm long, 1-2.5 mm thick, subquadrangular to somewhat flattened, ascending to erect or less commonly spreading-ascending; styles 1-4 (5) mm long; seeds wingless or winged only near tip, 1.5-2.3 mm long.— Warm desert shrub, cool desert shrub, mountain brush, pinyon-juniper, ponderosa pine, aspen, spruce, fir, and Douglas fir to alpine tundra communities, throughout Utah; Yukon Territory south to California and Arizona, and eastward to Oklahoma, Kansas, and Minnesota.

1. Flowers yellow or yellowish; fruits erect or nearly so; common .... *E. asperum* var. *purshii*
   Flowers orangish to burnt-orange; fruits ascending to spreading-ascending; common .... *E. asperum* var. *amoenum*

Var. *amoenum* (Greene) Reveal. [*Cheiranthus nivalis* var. *amoenus* Greene; *Cheirinia amoena* (Greene) Rydb.; *E. wheeleri* Rothrock; *Cheirinia wheeleri* (Rothrock) Rydb.] Common throughout southern portions of state; California eastward to Colorado.

Var. ***purshii*** Durand. [*Cheiranthus capitatus* Dougl. ex Hook.; *E. elatum* Nutt. ex Torr. & Gray; *E. capitatum* (Dougl.) Greene; *Cheiranthus elatus* (Nutt.) Greene; *Cheiranthus asperrimus* Greene; *Cheiranthus argillosus* Rydb.; *Cheiranthus bakeri* Greene; *Cheirinia elata* (Nutt.) Rydb.; *E. asperrimum* (Greene) Rydb.; *E. oblanceolatum* Rydb.; *E. bakeri* (Greene) Rydb.; *E. aridum* A. Nels.; *E. capitatum* var. *argillosum* (Greene) R. J. Davis] Common throughout most of state, but particularly common in northern portion; Yukon Territory south to California and Arizona, east to Montana, Wyoming, Colorado, and New Mexico.

Erysimum cheiranthoides L. [*Cheirinia cheiranthoides* (L.) Link; *Cheiranthus cheiranthoides* (L.) Heller] Annual, stems simple or branched, 2-12 dm tall; leaves 2-8 cm long, 0.2-1.5 cm wide, linear to oblong, lanceolate or oblanceolate, entire or denticulate, green, pubescent with malpighian or Y-shaped hairs; racemes much elongating in fruit; pedicels 4-15 mm long, spreading-ascending, very slender; sepals 2-3 mm long, yellowish or greenish; petals 3-5 mm long, pale yellow; siliques 12-27 mm long, about 1 mm wide, subterete, ascending to erect; styles 0.8-1 mm long; seeds 1-1.2 mm long, not winged.— Moist places, in meadows and along roadsides in Cache and Wasatch counties, and to be expected elsewhere; widespread in North America; adventive from Eurasia. This plant is evidently uncommon to rare in Utah.

Erysimum inconspicuum (S. Wats.) MacMillan. [*E. asperum* var. *inconspicuum* S. Wats.; *E. parviflorum* Nutt. ex Torr. & Gray, not Pers.; *E. syrticolum* Sheldon; *Cheiranthus inconspicuus* (S. Wats.) Greene; *Cheirinia inconspicua* (S. Wats.) Rydb.; *Cheirinia syrticola* (Sheldon) Rydb.] Biennial or short-lived perennial with usually unbranched caudex, stems mostly 2-10 dm tall, usually simple; leaves 1.5-8 cm long, 0.2-0.8 cm wide, linear to oblong, elliptic, lanceolate or oblanceolate, pubescent with malpighian or Y-shaped hairs; racemes elongating in fruit; pedicels 3-8 mm long, ascending; sepals 4-7 mm long, greenish or purplish; petals (6) 7-10 (11) mm long, pale to bright yellow; siliques 15-50 mm long, 1-2 mm thick, quadrangular, erect or ascending; styles 1-1.5 mm long; seeds about 1.5 mm long, not winged.— Sagebrush and aspen-spruce communities at middle elevations in Garfield, Wasatch, and Washington counties, and to be expected elsewhere; Alaska and Yukon south to Oregon, Utah, and Colorado, and east to central Canada and the north-central states. This species resembles *E. asperum* in general habit, but is more restricted in its distribution in Utah.

Erysimum repandum L. [*Cheirinia repanda* (L.) Link] Annual, stems 0.8-3 (5) dm tall, simple to much-branched; leaves 0.7-11 (15) cm long, 0.1-0.8 (1.2) cm wide, oblong, oblanceolate to linear, pubescent with malpighian and Y-shaped hairs; pedicels 2-5 mm long, spreading, almost or quite as thick as the fruit; sepals 3.5-5.8 mm long, yellowish or greenish; petals 5.2-8 mm long, yellow; siliques 26-85 mm long, 0.9-1.5 mm thick, quadrangular, spreading to ascending, rarely descending; styles 1-3 mm long; seeds ca 1 mm long, not winged.— Disturbed sites from 1300 to 1950 m elevation in Beaver, Grand, Juab, Millard, Salt Lake, Sanpete, Utah, and Washington counties, and to be expected elsewhere; widespread in North America; adventive fom Europe.

EUCLIDIUM R. Br.

Nom. Cons.

Plants pubescent with forked hairs, annual, from taproots; leaves alternate, simple, entire to remotely serrulate, petiolate to subsessile, not auriculate; flowers solitary and axillary or subaxillary, or borne in elongate racemes, pedicels sometimes subtended by bracts; sepals 4, caducous; petals 4, white, minute; stamens 6; style very short atop beak of fruit, stigma bilobed; fruit a silicle, bilocular, tardily dehiscent; seed 1 per locule.

A Eurasian genus of 2 species.

Euclidium syriacum (L.) R. Br. [*Anastatica syriaca* L.] Plants 0.4-5 dm tall, simple to much-branched, pubescent with forked hairs; leaves mainly cauline, 0.7-6.5 cm long, 0.2-1.7 cm wide, oblanceolate to elliptic or lanceolate, pubescent; pedicels 0.5-1 mm long, ascending to erect, pubescent; sepals 0.7-0.9 mm long, tinged with purple; petals 0.8-1.1 mm long, white, spatulate, erect; silicles (including beak) 2.8-4 mm long, body 1.2-2 mm wide, pubescent with simple or forked hairs, beak 1.2-1.6 mm long; style short or obsolete.— Roadsides, vacant lots, and dry foothills in Box Elder, Salt Lake, Summit, and Utah counties, and likely elsewhere; Idaho, Washington; adventive from Europe.

Glaucocarpum Rollins

Plants glabrous and glaucous, perennial from a branching caudex; leaves alternate, simple, entire or sparingly dentate, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow; stamens 6, paired ones united by filaments and anthers their entire length; style short, stigma capitate, entire, unexpanded; fruit a subsessile to sessile silique, many times longer than broad, slightly flattened, valves strongly 1-nerved; seeds uniseriate.

A monotypic genus endemic to Utah.

Rollins, R. C. 1938. *Glaucocarpum*, a new genus in the Cruciferae. Madroño 4:232-235.

Glaucocarpum suffrutescens (Rollins) Rollins. [*Thelypodium suffrutescens* Rollins in Graham] Plants perennial from a branching caudex forming small clumps, stems 1-2.5 dm tall, glabrous, lacking basal leaves; leaves (0.7) 1-2.5 cm long, 0.3-1 cm wide, elliptic to lanceolate or oblanceolate, short petiolate to subsessile, not auriculate; pedicles (2.5) 3-12 mm long, curved-ascending to erect, glabrous; sepals 4-6 mm long, yellowish or greenish; petals 9-11 mm long, yellow, spatulate, ascending to spreading; siliques 10-20 mm long, 1.2-3 mm wide, flattened, erect, glabrous; styles (0.5) 1-2 mm long, stigma capitate, entire; seeds 4-8 per locule.— Local and infrequent on calcareous shale of the Green River Formation, west of Willow Creek in the vicinity of Big Pack Mountain, from 1645 to 1825 m elevation, Uintah County; endemic.

This genus is the only one strictly endemic to the state.

Halimolobos Tausch

Plants pubescent with simple, forked, and branched hairs, (annual) biennial or perennial, arising from a taproot; leaves alternate or basal and still alternate, simple, dentate to subentire, tapering to base or cauline sessile and auriculate; flowers racemose, pedicels ascending, not subtended by bracts; sepals 4; petals 4, white; stamens 6; styles prominent, stigma small, entire; fruit a sessile, slender silique, many times longer than broad, terete to quadrangular, valves strongly 1-nerved; seeds biseriate, numerous.

A genus of perhaps 15 species of North and South America.

Rollins, R. C. 1943. Generic revisions in the Cruciferae: *Halimolobos*. Contr. Dudley Herb. 2: 241-265.

Rollins, R. C. 1952. A note on *Halimolobos*. Rhodora 54:161-163.

Halimolobos virgata (Nutt.) O. E. Schulz. [*Sismybrium virgatum* Nutt. ex Torr. & Gray; *Hesperis virgata* (Nutt.) Kuntz; *Stenophragma virgatum* (Nutt.) Greene; *Arabis brebneriana* A. Nels.; *Pilosella virgata* (Nutt.) Rydb.; *P. stenocarpa* Rydb.; *Arabidopsis virgata* (Nutt.) Rydb.; *Arabidopsis stenocarpa* (Rydb.) Rydb.] Biennial but occasionally flowering the first year, stems 1-3.5 dm tall, simple or branched, pubescent with mixed simple, forked, and branched hairs at least below; basal leaves 3-6 cm long, 0.5-1.8 cm wide, oblanceolate to lanceolate, denticulate to dentate, rarely entire; cauline leaves several, reduced upwardly, at least uppermost both sessile and auriculate; pedicels 7-11 mm long, ascending, glabrous or puberulent; sepals 2.5-3 mm long, greenish, pubescent; petals 4-4.5 mm long, white, veins often suffused with pink or purple, usually erect; siliques 15-40 mm long, mostly 1-1.5 mm wide, subquadrangular, erect, valves glabrous, strongly nerved; styles 0.2-0.5 mm long; seeds irregularly biserrate.— Grassy meadows and shrublands along the north slope of the Uinta Mountains in Daggett (US) and Summit counties; Colorado, Wyoming, Idaho, and northward to Alberta and Saskatchewan.

The number of generic segregates listed above are an indication of the difficulties involved in placing this unusual species in a genus. It simulates an *Arabis*, from which it is outwardly separable only with difficulty, but on technical grounds is probably more closely allied to *Sismybrium* in a broad sense. Our Utah material, and that from southwestern Wyoming, differs slightly from that found elsewhere and may deserve varietal recognition.

HESPERIS L.

Plants pubescent with simple and forked hairs, perennial, from taproots; leaves alternate, simple, sinuate-dentate or serrate, mainly cauline, petiolate to subsessile, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, pink to lavender or white; stamens 6, filaments lacking glandular processes; styles obsolete, stigma bilobed, massive; fruit a silique, many times longer than broad, subterete, tardily dehiscent, valves 1 (3)-nerved; seeds uniseriate.

A Eurasian genus of perhaps 24 species, many cultivated.

Hesperis matronalis L. Dame's Violet; Sweet Rocket. Plants perennial with one to several stems, these simple or branched, mostly 5-12 dm tall or more, pubescent with mixed forked and simple hairs; leaves 2-15 (20) cm long, 0.6-3.5 (4) cm wide, ovate-lanceolate to elliptic or lanceolate, sinuate-dentate to serrate, pubescent; pedicels 8-21 mm long, ascending to spreading, pubescent; sepals 6.5-8 mm long, often suffused with red or purple, pubescent; petals 15-25 mm long, pink to lavender or white, obovate, spreading; siliques 31-100 mm long, 1-2 mm wide, subterete, erect or ascending, puberulent; styles obsolete, stigma deeply bilobed; seeds numerous in each locule.— Cultivated ornamental, persisting and escaping, now widely established in cultivated lands especially along irrigation canals at mid elevations in Cache, Utah, and Summit counties, and expected to be established elsewhere; introduced from Europe.

HUTCHINSIA R. Br.

Plants glabrous, annual or winter annual, from taproots; leaves alternate, simple, entire to pinnatifid, petiolate to sessile, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white; stamens 6, filaments lacking glandular processes; styles obsolete or very short, stigma capitate, entire; fruit a silicle, only somewhat longer than broad, strongly compressed at right angles to septum, valves reticulately veined; seeds several.

A genus of 6 Eurasian and 1 North American species.

Hutchinsia procumbens (L.) Desv. [*Lepidium procumbens* L.; *Hymenolobus divaricatus* Nutt. ex Torr. & Gray; *Hymenolobus erectus* Nutt. ex Torr. & Gray] Slender, diminutive annuals, stems glabrous, simple or more commonly branched, 0.5-3 dm long, erect or prostrate; leaves basal and cauline, 0.5-3 cm long, 0.1-1.3 cm wide, ovate to lanceolate, oblanceolate, or nearly linear, entire to pinnatifid, petiolate to subsessile; pedicels 3-8 mm long, ascending to spreading-ascending, glabrous; sepals 0.7-1.1 mm long, greenish or purplish, glabrous; petals 0.8-1.3 mm long, white, spatulate, rounded to retuse; silicles 2.4-4.2 mm long, 1.5-2 mm wide, elliptic to obovate, truncate, rounded, or somewhat emarginate, glabrous; styles up to 0.2 mm long; seeds several per locule.— Moist to dry sites, hanging gardens, drainage banks, sidewalks, roadsides, playas, and peat bogs from 850 to 1830 m elevation in Garfield, Salt Lake, San Juan, Utah, and Washington counties; widely distributed in North America; Eurasia.

ISATIS L.

Plants pubescent with long simple hairs at least below, biennial or short-lived perennial, from strong taproots; leaves simple, alternate, basal petiolate, cauline hastately-auriculate; flowers racemose or paniculate, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow; stamens 6, filaments lacking glandular processes; styles obsolete, bilobed stigma sessile; fruit a silicle, samaroid, indehiscent, flattened at right angles to the plane of the partition (which is lacking), more or less reticulate; seeds solitary.

A genus of about 30 Eurasian species, many in cultivation.

Isatis tinctoria L. Dyer's Woad. Plants erect, stems 3.5-10 dm tall or more, glabrous throughout or hirsute with long simple hairs at base; basal leaves 3.5-15 (18) cm long, 0.8-4 cm wide, oblanceolate to elliptic, subentire to crenulate, ciliate to pilose with simple hairs; cauline leaves gradually reduced upwards, lanceolate to elliptic, entire, hastately-auriculate, glabrous or pilose on veins beneath and often ciliate; pedicels 4.5-9 mm long, reflexed, glabrous; sepals 1.8-2.3 mm long, yellowish, glabrous; petals 3-4.2 mm long, yellow, spatulate, rounded; silicles mostly 10-18 mm long, 4-7 mm wide, cuneate-oblong to oblanceolate, more or less truncate-rounded apically, glabrous; stigmas sessile.— Roadsides, abandoned fields, and dry foothills from 1350 to 1980 m elevation in Box Elder, Cache, Davis, Sanpete, Summit, Utah, and Weber counties; widely established in the United States; adventive from Europe.

This plant is the source of a blue dye and was thus widely cultivated in the recent past. It seems to be spreading outwardly from its initial foci in Box Elder County, where it has been established as a weed since at least 1947.

LEPIDIUM L.

Plants glabrous or with simple hairs, annual, biennial or perennial, from taproots; leaves alternate or basal and still alternate, simple and entire or variously toothed or bi- or tripinnatifid, petiolate or sessile, auriculate in some; flowers racemose, pedicels lacking bracts; sepals 4, caducous or persistent; petals 4, yellow or white, infrequently lacking; stamens 6, rarely 2 or 4, filaments lacking glandular processes; style obsolete or well developed, stigma capitate; fruit a silicle, usually less than twice longer than broad, compressed at right angles to septum, dehiscent, valves more or less reticulately veined; seeds 1 per locule. (Note: Measurement of silicle length includes style.)

A complex genus of perhaps 150 species found throughout the world, many as weeds.

Hitchcock, C. L. 1936. The genus *Lepidium* in the United States. Madroño 3:265-320.

Mulligan, G. A. 1961. The genus *Lepidium* in Canada. Madroño 16:77-90.

1. Cauline leaves perfoliate-clasping or auriculate 2
Cauline leaves petiolate to sessile but not auriculate or clasping 3

2(1). Petals 2-2.5 mm long, white; cauline leaves lanceolate to lance-oblong, merely auriculate .... *L. campestre*
Petals 1-2 mm long, yellow; cauline leaves oval to ovate, pseudoperfoliate .... *L. perfoliatum*

3(1). Plants arising from thickened, well-developed caudices; leaves all entire; stems seldom more than 2.5 dm tall; plants rare, south-central to northern Utah 4
Plants from simple or branched caudices, these seldom thickened; leaves entire, toothed or pinnatifid; stems short to long; plants widespread 5

4(3). Leaves linear; petals more than 3 mm long; plants of xeric shales, known only from Duchesne County .... *L. barnebyanum*
Leaves oblanceolate to elliptic; petals less than 3 mm long; plants of moist meadows from Beaver County northward but not of Duchesne County ......

.... *L. integrifolium*

5(3). Styles 0.3-1 mm long; plants perennial or biennial 6
Styles obsolete or only up to 0.3 mm long; plants annual, rarely if ever biennial 7

6(5). Stems woody well above base; petals mostly 3 mm long or more; silicles 4.5-7.5 mm long, obovate; plants of Washington County .... *L. fremontii*
Stems slightly if at all woody above base; petals mostly less than 3 mm long (but sometimes longer); silicles 2-4 mm long, ovate; plants almost cosmopolitan in Utah .... *L. montanum*

7(5). Sepals persistent, enclosing mature silicle; silicles plainly reticulate; pedicels narrowly wing-margined; plants evidently rare .... *L. strictum*
Sepals deciduous at or shortly following anthesis; silicles plainly to slightly reticulate; pedicels terete to strongly flattened; plants at least locally common 8

8(7). Fruits emarginate and with prominent, acute, and divergent toothlike apices .... *L. dictyotum*
Fruits emarginate but lobes on each side of sinus neither acute nor divergent 9

9(8). Pedicels much flattened, about twice broader than thick 10
Pedicels not strongly flattened, not twice as broad as thick 11

10(9). Plants short-hirsute to hispid hairy; silicles pubescent .... *L. lasiocarpum*
Plants softly hairy; silicles glabrous or pubescent .... *L. densiflorum*

11(9). Petals lacking, or, if present, generally shorter than sepals; silicles oblong-obovate to obovate .... *L. densiflorum*
Petals present and usually surpassing sepals; silicles elliptic-rotund to orbicular .... *L. virginicum*

Lepidium barnebyanum Reveal. [*L. montanum* ssp. *demissum* C. L. Hitchc., not *L. demissum* C. L. Hitchc.] Perennial, densely pulvinate-cespitose, from a thickened branched caudex, clothed with marcescent leaf bases; stems erect, 0.7-1.2 dm tall, subglabrous or minutely recurved scaberulous, simple or branched from the upper axils; basal leaves 1-4 cm long, 0.1-0.2 (0.3) cm wide, somewhat flattened and minutely wing-margined, scaberulous; sepals 2-2.3 mm long, greenish, glabrous or puberulent; petals 3.5-4.2 mm long, white, obovate, spreading; stamens 6; silicles 3-6.2 mm long, 3-4 mm wide, lanceolate to elliptic, glabrous, plane, wingless; styles 0.5-1.2 mm long.— White (Green River) shale outcrops, Indian Canyon, Duchesne County; known only from the type locality; endemic.

Lepidium campestre (L.) R. Br. [*Thlaspi campestre* L.] Annual, lacking a caudex, stems 1.5-6 dm tall, hirtellous throughout with simple hairs; basal leaves 3-12 cm long, 0.8-1.5 cm wide, oblanceolate, entire or variously lobed; cauline leaves numerous, reduced upwards, becoming sessile and auriculate, usually denticulate; pedicels mostly 4-7 mm long, spreading, slightly flattened, hirtellous; sepals 1.3-2 mm long, greenish or variously tinged, hirtellous; petals 1.7-2.5 mm long, white, spatulate, ascending; stamens 6; silicles 5-6 mm long, oblong-ovate, glabrous or puberulent, concave, wingless, slightly emarginate; styles 0.2-0.6 mm long.— Roadsides and disturbed sites from 1300 to 2000 m elevation in Salt Lake, Summit, and Utah counties, and probably widespread in the state; widely established in North America; Asia.

Lepidium densiflorum Schrad. Annual, lacking a caudex, stems 0.3-5 dm tall or more, densely finely hairy to puberulent throughout; basal leaves 1.2-11 cm long, 0.3-2.2 cm wide, oblanceolate, entire and more commonly pinnately lobed; cauline leaves several to many, reduced upwards, petiolate to sessile, not auriculate, lobed, toothed or entire; pedicels 1.5-3 mm long, spreading to ascending, subterete to conspicuously flattened, glabrous to puberulent; sepals 0.6-1.1 mm long, often purplish, glabrous; petals 0.7-1 mm long, white, narrowly oblong, sometimes lacking; stamens 2; silicles 2.5-3.5 mm long and about as wide, elliptic to oval or obovoid, glabrous or rarely pubescent, shallowly notched apically, teeth rounded; style lacking.— Widespread from low to moderate elevations in Utah; North America; Eurasia. Our material is separable into three more or less distinctive variants.

1. Silicles pubescent, the pedicels usually somewhat flattened, especially on lower side; plants evidently rare .... *L. densiflorum* var. *pubicarpum*
Silicles glabrous, pedicels definitely flattened or else subterete; plants common 2

2(1). Pedicels subterete, silicles averaging less than 3 mm long; plants commonly of waste places .... *L densiflorum* var. *densiflorum*
Pedicels definitely flattened, especially on upper side, silicles averaging at least 3 mm long; plants often growing in indigenous communities .... *L. densiflorum* var. *ramosum*

Var. ***densiflorum*** [*L. neglectum* Thell.; *L. bourgeauanum* Thell.; *L. densiflorum* var. *bourgeauanum* (Thell.) C. L. Hitchc.] Weedy species usually of waste places, less commonly of indigenous plant communities, of Duchesne, Grand, Iron, Kane, Millard, Piute, Sevier, Uintah, Utah, and Washington counties, possibly cosmopolitan; range of species.

This variety is abundant in Utah; we have not been able to distinguish the var. *bourgeauanum* from among this material.

Var. ***pubicarpum*** (A. Nels.) Thell. [*L. pubicarpum* A. Nels.] Uncommon in dry sites in Salt Lake and Sanpete counties, and undoubtedly elsewhere; Washington to Montana and south to California.

Var. ***ramosum*** (A. Nels.) Thell. [*L. ramosum* A. Nels.; *L. densiflorum* var. *pubicaule* Thell.] Common, usually in indigenous communities, in Emery, Garfield, Grand, Kane, San Juan, Sanpete, Uintah, and Utah counties, and probably elsewhere; Wyoming south to New Mexico west to California.

Lepidium dictyotum A. Gray. [*L. dictyotum* var. *macrocarpum* Thell.] Annual, lacking a caudex, stems 0.2-1.5 dm tall, pubescent; basal leaves usually pinnatifid with 2-5 pairs of linear lobes; cauline leaves mostly entire, reduced upwards; pedicels 1.5-3.5 mm long, flattened, spreading to reflexed; sepals 0.7-1 mm long, greenish, pubescent; petals 1-1.2 mm long, white, oblong, or usually lacking; stamens typically 4; silicles 3.2-4.5 mm long, 2-2.5 mm wide, ovate, glabrous or hirtellous, notched apically, teeth prolonged and usually divergent, acute; style lacking.— Evidently rare in Utah, reported from Salt Lake County by Hitchcock (1936, cited above).

Lepidium fremontii S. Wats. Perennial subshrubs, definitely woody above base, stems mostly 3-8 dm tall, glabrous and glaucous; leaves cauline, mostly 1.5-5 (8) cm long, pinnatifid into linear-oblong, acute lobes up to 2 mm wide, becoming simple above, not auriculate; bracts subtending to curved-ascending, glabrous; sepals 1.6-2.1 mm long, green, glabrous; petals 3-4.5 mm long, white, obovate; stamens typically 6; silicles 4.5-7.5 mm long, 5.2-6.5 mm wide, obovate, glabrous, slightly notched apically; styles 0.4-1.3 mm long.— Blackbrush, creosote brush, and other warm desert shrub communities from 600 to 1525 m elevations in Washington County; Arizona, Nevada, and California.

This species is obviously related to *L. montanum* (q.v.), but differs in being woody, having distinctive bracts in the inflorescence, and in having larger, obovate silicles.

Lepidium integrifolium Nutt. [*L. utahense* M. E. Jones; *L. zionis* A. Nels.; *L. montanum* var. *integrifolium* (Nutt.) C. L. Hitchc.] Perennial, cespitose, from a thickened, usually branched caudex, more or less clothed with marcescent leaf bases, stems decumbent-ascending, 1.5-2.5 dm tall, minutely puberulent, simple or branched from upper axils; basal leaves 3-8.5 cm long, 0.6-2.5 cm wide, elliptic to oblanceolate, entire; cauline leaves mostly 1-4 cm long, 0.2-1.2 cm wide, gradually reduced upwards, glabrous or nearly so; pedicels 5-8.5 mm long, spreading to ascending, puberulent; sepals 1.5-2 mm long, greenish, glabrous or pubescent; petals 2.7-3.1 mm long, white, obovate; stamens typically 6; silicles 3-4.2 mm long, 1.7-2.7 mm wide, ovate to lance-ovate, glabrous, plane, wingless; styles 0.4-0.7 mm long.— Saline meadows at low to moderate elevations in Beaver, Rich, Sevier, and Uintah counties; Wyoming.

This distinctive entity has been collected only rarely possibly because the habitat type has been exploited as marginal pastureland in Utah and Wyoming.

Lepidium lasiocarpum Nutt. ex Torr. & Gray. Annual, lacking a caudex, stems 0.2-3 dm tall or more, hispidulous to distinctly hispid with simple hairs; basal leaves mostly 1-8.5 cm long, 0.3-0.9 cm wide, oblanceolate, pinnatifid or merely lobed or toothed; cauline leaves few to several, reduced upwards, petiolate to sessile, not auriculate; pedicels 1.5-5 mm long, spreading to ascending, conspicuously flattened, usually puberulent to hispidulous; sepals 1-1.2 mm long, greenish or reddish to purplish, glabrous; petals 1-1.3 mm long, white, narrowly oblong, sometimes lacking; stamens 2 or 4; silicles 3.4-4.5 mm long, 2.7-4 mm wide, elliptic to rotund or obovate, hispidulous, notched apically, teeth sometimes elongate-winged, rounded; style lacking or nearly so.— Widely distributed mostly in the southern two-thirds of Utah; California eastward into New Mexico and Texas.

Plants with somewhat attenuate apical teeth on the silicles approach *L. dictyotum*, and possibly they account for reports of that entity from Utah.

Two scarcely distinguishable varieties are known from Utah:

1. Pedicels glabrous or merely puberulent on lower side; stems, at most, hispidulous .... *L. lasiocarpum* var. *georginum*
   Pedicels hispidulous on lower side; stems definitely hispid .... *L. lasiocarpum* var. *lasiocarpum*

Var. *georginum* (Rydb.) C. L. Hitchc. [*L. georginum* Rydb.; *L. lasiocarpum* ssp. *georginum* (Rydb.) Thell.] Warm desert shrublands and lower pinyon-juniper woodlands in Grand, Kane, San Juan, Tooele, Uintah, and Washington counties; Arizona westward to California.

Var. *lasiocarpum* [*L. palmeri* S. Wats.; *L. lasiophyllum* Brandegee; *L. lasiocarpum* ssp. *palmeri* (S. Wats.) Thell.; *L. lasiocarpum* ssp. *lasiophyllum* (Brandegee) Thell.] Warm to cool desert shrublands in Kane, Millard, Utah, and Washington counties; Arizona westward to California.

Lepidium montanum Nutt. Perennial or less commonly biennial herbs or rarely suffrutescent, seldom definitely woody above base, stems 0.3-12 dm tall or more, glabrous or variously puberulent to hirtellous; leaves basal or basal and cauline, 0.5-12.5 cm long, 0.1-2.5 cm wide, variously shaped, entire to pinnatifid, often at least uppermost cauline ones simple; bracts subtending branches of inflorescence seldom more than 1 cm long; pedicels 3-8 mm long, spreading to ascending, glabrous or puberulent; sepals 1.2-1.7 mm long, green or variously tinged, glabrous or puberulent; petals 2.5—3.5 mm long, white, obovate to spatulate; stamens typically 6; silicles 2.8-4.1 mm long, 2.1-2.5 mm wide, ovate to elliptic, glabrous or rarely puberulent; styles 0.3-0.9 mm long.— Low to high elevations throughout Utah; Oregon to Wyoming southward to California, Arizona, New Mexico, and Texas.

There is an amazing amount of variation

within *L. montanum* as interpreted herein. The more stable phases have been treated previously either as species or as varieties. There is some justification for recognizing all of these entities at the specific level, but the convenience of having an inclusive species with several variants seems to best represent the situation within Utah.

1. Plants mostly 6-12 dm tall; cauline leaves simple, toothed or entire, often more than 4 mm wide; flowering from midsummer to autumn; eastern to southeastern Utah .... *L. montanum* var. *spathulatum*
   Plants usually less than 6 dm tall; cauline leaves various, if simple and entire then usually less than 4 mm wide; flowering in springtime and midsummer (at higher elevations); distribution various 2

2(1). Basal leaves well developed, usually over 5 cm long and 0.6 cm wide; cauline leaves few, reduced upwards; plants usually montane 3
   Basal leaves poorly, if at all, developed, usually less than 5 cm long and 0.6 cm wide; cauline leaves numerous to few, gradually reduced upwards; plants seldom montane 4

3(2). Stems puberulent almost or quite throughout .... *L. montanum* var. *alpinum*
   Stems glabrous almost or quite throughout .... *L. montanum* var. *heterophyllum*

4(2). Stems glabrous or essentially so (rarely puberulent); plants somewhat woody at the base 5
   Stems puberulent almost or quite throughout; plants herbaceous or somewhat woody at the base 6

5(4). Plants (0.7) 1-6 (10) dm high; basal leaves divided, not entire; widespread in eastern, southeastern and southern Utah .... *L. montanum* var. *jonesii*
   Plants 0.2–0.5 (0.7) dm high; basal leaves entire or some divided; rare and local, Aquarius Plateau, Garfield County .... *L. montanum* var. *neeseae*

6(4). Plants perennial, the caudex woody; silicles puberulent; stems 0.5-1 dm tall; restricted to Kane County .... *L. montanum* var. *stellae*
   Plants biennial or perennial, the caudex lacking or only slightly woody; silicles glabrous; stems often over 1 dm tall; widespread in western Utah ....
   .... *L. montanum* var. *montanum*

Var. alpinum S. Wats. [*L. scopulorum* M. E. Jones; *L. heterophyllum* M. E. Jones] Plants of rocky or sandy places at moderate to high elevations in Box Elder and Salt Lake counties; endemic.

Var. *heterophyllum* (S. Wats.) C. L. Hitchc. [*L. integrifolium* var. *heterophyllum* S. Wats.] Oak brush community, Cedar Canyon, Iron County. Endemic.

Var. *jonesii* (Rydb.) C. L. Hitchc. [*L. jonesii* Rydb.; *L. crandallii* Rydb.; *L. tortum* L. O. Williams; *L. alyssioides* var. *jonesii* (Rydb.) Thell.; *L. alyssioides* var. *stenocarpum* Thell.] This is the abundant spring-flowering form of *L. montanum* of the Colorado drainage system. Mostly of middle to low elevations in Carbon, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Uintah, Utah, Washington, and Wayne counties; Arizona and Nevada eastward to Colorado.

Var. *montanum*. [*L. corymbosum* Hook. & Arn.; *L. utaviense* Regal; *L. brachybotryum* Rydb.; *L. philonitrum* Nels. & Macbr.; *L. albiflorum* Nels. & Macbr.; *L. montanum* var. *stenocarpum* Thell.; *L. scopulorum* f. *nanum* Thell.; *L. montanum* var. *canescens* (Thell.) C. L. Hitchc.] The phase distinguished as var. *canescens* by Hitchcock passes into var. *montanum* through a series of morphological intermediates; thus it is placed here in synonymy with var. *montanum*. The var. *montanum* is a plant of lower elevations in Box Elder, Duchesne, Iron, Juab, Millard, Piute, Sevier, Summit, Tooele, Utah, and Washington counties; Idaho and Wyoming south to Arizona, Nevada, and California.

Var. *neeseae* Welsh & Reveal, var. nov. Planta similis *Lepidio montano* var. *stellae* sed differt in caudicibus non ligneis, foliis basalibus et integris vel lobatis, et siliquis glabris. Holotype: Utah, Garfield Co., T.32S., R.3E., sec. 35, 14 mi due north of Escalante at Hell's Backbone, 2745 m, Neese & White 3332, 23 June 1977 (BRY, Isotypes to be distributed). Paratype: Garfield Co., T.33S., R.3E., sec 35, 1 mile due southeast of Hell's Backbone, 2745 m, Neese & White 3944, 3 Aug. 1977 (BRY). The variety is named to honor Elizabeth Neese, ardent collector and student of the Henry Mountains flora.

Var. ***spathulatum*** (B. L. Robinson) C. L. Hitchc. [*L. scopulorum* var. *spathulatum* B. L. Robinson. *L. spathulatum* Vasey ex Robinson, not Philippi; *Thelypodium crenatum* Greene; *L. crenatum* (Greene) Rydb.; *L. vaseyanum* Thell.; *L. montanum* var. *eastwoodiae* sensu Utah material; *L. montanum* var. *alyssioides* sensu Utah material] This is the tall phase of the species which flowers in midsummer and autumn in southeastern Utah, in Garfield, Grand, Kane, San Juan, and Uintah counties; Colorado.

This variant is sufficiently distinct from the body of the remaining varieties of *L. montanum* to be recognized at the specific level. If that is done, the correct name at the specific level would be *L. crenatum*.

Var. ***stellae*** Welsh & Reveal, var. nov. Plantis similis *Lepedio montano* var. *montano* sed differt in siliculis puberulentis et caudicibus bene evolutis. Type: Kane County, Utah, along Cottonwood Wash Road, 6.4 miles south of Cannonville, on reddish clay soil near white barren shale outcrops south of the road, associated with *Artemisia*, *Juniperus*, and *Lesquerella tumulosa* at about 1700 m elevation, 29 May 1976, Reveal & Reveal 4454. Holotypus, BRY. Isotyi, 15 to be distributed from US. Paratype: Welsh & Welsh 12841 (BRY).

The variety is named to honor Stella L. T. Welsh, the cocollector, with the senior author, of this plant in June of 1975.

Lepidium perfoliatum L. Peppergrass. Plants annual, lacking a caudex, stems 0.7-4 (6) dm tall, hirtellous below, glabrous and glacous above; basal leaves 0.8-15 cm long, 0.2-2.8 cm wide, bi- or tripinnatifid into narrow segments; cauline leaves with lowermost like basal ones, these transitional upwardly into entire and falsely perfoliate-clasping ones; pedicels 3-6.5 mm long, spreading-ascending, glabrous, subterete; sepals 0.7-1.2 mm long, often purplish, glabrous or pubescent; petals 0.8-1.5 mm long, yellow, narrowly spatulate, ascending; stamens usually 6; silicles 3.5-4.3 mm long, 3.2-3.6 mm wide, oval to elliptic, glabrous, plane, wingless or essentially so, slightly emarginate; style 0.1-0.3 mm long.— Disturbed sites and dry slopes, flats, and other places at low elevations in Box Elder, Cache, Iron, Juab, Kane, Salt Lake, San Juan, Sanpete, Tooele, Utah, Washington, and Weber counties, and probably cosmopolitan; widespread in the United States; adventive from Europe.

Lepidium strictum (S. Wats.) Rattan. [*L. oxycarpum* var. *strictum* S. Wats.; *L. reticulatum* Howell; *L. pubescens* of authors, not Desv.] Annual, lacking a caudex, stems 0.5-2 dm long, prostrate to rarely erect, pubescent; basal leaves mostly 3-7 cm long, 1-2 cm wide, bipinnatifid; cauline leaves less divided, uppermost sometimes entire; pedicels mostly 2-3 mm long, ascending, flattened, and narrowly wing-margined; sepals 1-1.5 mm long, persistent, purplish, pubescent; petals minute or lacking; stamens 2; silicles 2.2-3.5 mm long, 2-3 mm broad, oval to oblong-ovate, planely reticulate, slightly winged, concave, notched apically; style lacking.— Apparently rare in Utah and possibly not a part of the continuing flora; cited by Hitchcock (1936) from Castle Gate, Carbon County, collected by Grant in 1900.

Lepidium virginicum L. Plants annual, lacking a caudex, stems 1.5-7 dm tall, pubescent throughout or glabrous above; basal leaves 1.3-15 cm long, 0.3-3.5 (5) cm wide, coarsely toothed to lobed; cauline leaves reduced upwards, uppermost usually entire; pedicels 2-6 mm long, spreading, terete or nearly so, pubescent or glabrous; sepals 0.6-1 mm long; petals 0.7-1.5 (3) mm long, white, spatulate, rarely lacking; silicles 2.5-4 mm long, 2.2-3.5 mm broad, elliptic to orbicular, usually glabrous, plane, notched apically; style lacking.— Roadside, trails, foothills, stream sides, and similar disturbed places from low to moderate elevations in Salt Lake, Utah, Wasatch, Washington, and Weber counties, and likely elsewhere; widely distributed in North America.

Our material belongs to var. *pubescens* (Greene) Thell. [*L. intermedium* var. *pubescens* Greene; *L. hirsutum* Rydb.], the combination made by Thellung annodating that by Hitchcock by thirty years, and thus making the change of authorship necessary here. Because it seems probable that other varieties will be found in the state, the following key is provided:

1. Silicles usually consistently longer than broad; stems usually hirtellous throughout; plants of eastern United States, adventive in our region .... *L. virginicum* var. *virginicum*
   Silicles usually about as long as broad; stems glabrous above or minutely puberulent throughout; plants indigenous 2

2(1). Pedicels and raceme-rachis minutely puberulent .... *L. virginicum* var. *pubescens*
   Pedicels and raceme-rachis glabrous .... *L. virginicum* var. *medium*

Var. ***medium*** (Greene) C. L. Hitchc. [*L. intermedium* A. Gray, not Richard; *L. medium* Greene; *L. glaucum* Greene; *L. idahoense* Heller] Reported from all states surrounding Utah on north and east, and to be expected here.

Var. ***pubescens*** (Greene) Thell. Distribution as given above.

Var. ***virginicum.*** Reported from scattered sites in the West and to be expected in Utah.

LESQUERELLA S. Wats.

Plants stellate pubescent annual (biennial) or perennial, arising from taproots; leaves basal and cauline, alternate, simple, tapering to base or merely sessile, nto auriculate; flowers racemose, pedicels straight, sigmoid, reflexed, spreading or ascending, not subtended by bracts; sepals 4, deciduous; petals 4, yellow, rounded; stamens 6, filaments lacking glandular processes; style slender, stigma capitate; fruit a sessile to substipitate silicle, less than twice longer than broad, varying in outline, compressed parallel or contrary to septum, valves veinless; seeds 2-10 per locule, biseriate.

A genus of about 80 species found in North and South America and just entering Asia.

Maguire, B., and A. H. Holmgren. 1951. Botany of the intermountain region—II. *Lesquerella.* Madroño 11:172-184.

Payson, E. B. 1921. A monograph of the genus *Lesquerella.* Ann. Missouri Bot. Gard. 8:1-3-236.

Rollins, R. C., and E. A. Shaw. 1973. The genus *Lesquerella* in North America. Cambridge, Mass.: Harvard University Press. 288 p.

1. Lowermost leaves narrow, mostly 1-5 mm wide, blade and petiole indistinct, or, if so, as in *L. rectipes*, plants tall and of low elevations, tufted at stem base; basal and cauline leaves alike in general shape .... KEY I
   Lowermost leaves often over 5 mm wide, blade distinct from petiole, forming a rosette; basal leaves clearly of a different shape from cauline leaves .... KEY II

Key I.

Basal and cauline leaves alike

1. Silicles and ovaries glabrous 2
   Silicles and ovaries stellate pubescent 4

2(1). Stems mostly 0.6-1.8 dm tall; silicle bodies 4 mm long or more; plants of San Juan County .... *L. fendleri*

Stems 0.1-0.5 dm tall; silicle bodies usually less than 4 mm long; plants of south-central Utah 3

3(2). Plants densely pulvinate-cespitose, cushionlike, with usually numerous caudex branches; restricted to white shale outcrops southeast of Cannonville, Kane County .... *L. tumulosa*
Plants cespitose in small compact to loose clumps, with one to several caudex branches; restricted to limestones on Paunsagaunt Plateau .... *L. rubricundula*

4(1). Plants definitely pulvinate-cespitose, usually less than 1 dm tall; styles mostly 1-2 mm long; known from Washington and Kane counties .... *L. arizonica*
Plants various, but if pulvinate-cespitose and less than 1 dm tall, then styles usually 2-4 mm long or more, or distribution otherwise 5

5(4). Plants usually less than 1 dm tall; basal leaves linear to narrowly spatulate; usually of middle to high elevations 6
Plants usually 1.5-2 dm tall or more; basal leaves spatulate to oblanceolate; usually of middle to lower elevations 7

6(5). Pedicels usually strongly S-shaped; inner basal leaves usually flat .... *L. alpina*
Pedicels usually straight or only slightly curved; inner basal leaves usually involute .... *L. intermedia*

7(5). Pedicels generally recurved or arched in fruit, or less commonly almost straight; blades of basal leaves rarely more than 4 mm wide .... *L. ludoviciana*
Pedicels more or less S-shaped; blades of basal leaves often more than 4 mm wide .... *L. rectipes*

Key II.

Basal and cauline leaves different

1. Plants slender annuals, stems erect or ascending, mostly 1-4 dm tall; restricted to Washington County .... *L. tenella*
Plants cespitose perennials, stems decumbent to erect, mostly less than 1 (1.5) dm tall; distribution otherwise 2

2(1). Plants with caudex definitely branched; known from low to moderate elevations of Duchesne, Emery, and Uintah counties .... *L. subumbellata*
Plants with caudex simple or rarely branched; distribution various, but usually of higher elevations 3

3(2). Silicles ellipsoid to subglobose or obovoid to obdeltoid, compressed contrary to septum 4
Silicles of various shape, but, if as above, compressed parallel to septum 5

4(3). Racemes loose to elongated in fruit, often secund; silicles sparingly pubescent with hairs 0.2-0.25 mm broad; plants of Wasatch and Uinta mountains .... *L. utahensis*
Racemes short and dense in fruit, not at all secund; silicles moderately pubescent with hairs 0.2-0.35 mm broad; plants of Wasatch Plateau southward .... *L. wardii*

5(3). Silicles ovoid, compressed at apex or margins; plants known from northern Wasatch Mountains, from Mt. Nebo northward .... *L. occidentalis*
Silicles various but not compressed at apex or margins; plants of various distribution 6

6(5). Basal leaves angular, blades usually deltoid or hastate, narrowed abruptly to petiole; plants of Rich and possibly Summit counties .... *L. prostrata*

Basal leaves not angular, blades elliptic to obovate, narrowed gradually to petiole; plants of various distribution 7

7(6). Silicles either definitely compressed at apex or truncate to emarginate apically; plants from Utah County southward 8

Silicles more or less acute apically; plants from Utah County northward 9

8(7). Silicles obcordate to obdeltoid, sparingly pubescent; largest basal leaves usually less than 1 cm wide; plants of Carbon, Emery, Sanpete, and Utah counties .... *L. hemiphysaria*

Silicles ellipsoid, densely pubescent; largest basal leaves usually more than 1 cm wide; plants of Garfield, Kane, Sevier, and Tooele counties .... *L. kingii*

9(7). Pedicels loosely S-shaped; silicles sparsely pubescent with appressed or erect hairs; caudex branches lacking conspicuous leaf scars and bases; plants of Cache and Rich counties .... *L. multiceps*

Pedicels straight or curved; silicles densely pubescent with erect hairs; caudex branches with conspicuous scars and/or leaf bases; plants of Davis, Salt Lake, Utah, and Wasatch counties .... *L. garrettii*

Lesquerella alpina (Nutt.) S. Wats. Perennial, arising from simple or branched caudices, these often clothed with marcescent leaf-bases; herbage pubescent with stellate, 4-7-branched hairs; stems 0.1-1 dm tall, rarely more, erect, simple; basal leaves mostly 0.5-5 cm long, 0.1-0.4 cm wide, linear to very narrowly spatulate, gradually narrowed to base; cauline leaves 0.5-2 cm long (or more), 0.1-0.3 cm wide; pedicels 4-10 mm long or more, straight, curved, or S-shaped; sepals 3.5-6 (7) mm long; petals 4-8 mm long, yellow, spatulate; silicles (excluding style) mostly 3-5 mm long, sessile or subsessile, ovoid, more or less compressed apically, valves pubescent externally and sometimes internally also; styles mostly 2-4 mm long; ovules 2-6 per locule.— Ridge tops and rocky slopes from 1830 to 3050 m elevation in central and northeastern Utah.

Two varieties which lack definite diagnostic criteria are represented among our materials.

1. Leaves spatulate, at least some; perhaps not distinct from the next .... *L. alpina* var. *alpina*

Leaves uniformly narrow, linear to linear-spatulate .... *L. alpina* var. *parvula*

Var. *alpina.* [*Vesicaria alpina* Nutt. ex Torr. & Gray; *L. spatulata* Rydb.; *L. curvipes* A. Nels.; *L. alpina* var. *spatulata* (Rydb.) Payson; *L. condensata* var. *laevis* Payson; *L. alpina* var. *laevis* (Payson) C. L. Hitchc.] Ridgetops and alpine areas from 2200 to 3050 m elevation in Uintah and Sanpete counties; widespread northward to Alberta and Saskatchewan.

Var. *parvula* (Greene) Welsh & Reveal, stat. nov., based on *Lesquerella parvula* Greene, Pittonia 4:308. 1901. [*L. alpina* ssp. *parvula* (Greene) Rollins & Shaw] Ridgetops and alpine to subalpine areas from 1830 to 2600 m elevation in Duchesne and Daggett counties; Colorado and Wyoming.

It seems probable that all the Utah material designated as *L. alpina* might belong only to var. *parvula*. The var. *condensata* (A. Nels.) C. L. Hitchc. is to be sought in extreme northern Daggett County; it is currently known from just north of the Utah line in Uinta County, Wyoming. The var. *condensata* is a small, tufted plant with the stems barely exserted beyond the leaves.

Lesquerella arizonica S. Wats. [*L. arizonica* var. *nudicaulis* Payson] Perennial, more or less pulvinate-cespitose, with few to several (or many) caudex branches, these often with marcescent leaf-bases; herbage densely pubescent with stellate hairs; stems 0.2-1 dm tall, rarely more, erect, simple; basal leaves 0.5-3.5 cm long, 0.1-0.4 cm wide, oblanceolate to spatulate, gradually narrowed to base; cauline leaves 0.5-2.5 cm long or more, 0.1-0.3 cm wide; pedicels 3-10 mm long or more, straight or curved, ascending; sepals 4-6.5 mm long; petals 5.5-7 mm long, yellow, suborbicular; silicles (excluding style) 3-5 mm long, sessile or substipitate, ovoid to ellipsoid, rounded and compressed apically, valves pubescent externally; styles 0.5-2 (4) mm long; ovules 2-5 (8) per locule.— Mountain brush, sagebrush, and pinyon-juniper communities from 1280 to 2750 m elevation in Kane and Washington counties; Arizona.

Lesquerella fendleri (A. Gray) S. Wats. [*Vesicaria fendleri* A. Gray; *V. stenophylla* A. Gray; *L. foliacea* Greene; *L. stenophylla* (A. Gray) Rydb.; *L. praecox* Woot. & Standl.] Perennial, cespitose, caudex simple or few- to several-branched, branches naked or with few marcescent leaf-bases; herbage usually densely pubescent with stellate hairs; stems 0.5-2.5 dm tall, rarely more, erect to decumbent, simple; basal leaves 1-4 cm long, 0.1-0.6 cm wide, elliptic to oblanceolate, gradually tapering to the base; cauline leaves 0.4-2 (2.5) cm long, mostly 0.1-0.5 mm wide; pedicels 7-15 (20) mm long, straight or curved to S-shaped, spreading to suberect; sepals 4.5-8 mm long; petals 6-12 mm long, yellow, obovate; silicles (excluding style) 4.5-8 mm long, sessile or subsessile, ellipsoid to ovoid, rounded apically, the valves glabrous; styles 2-6 mm long; ovules 6-16 per locule.— Warm desert, salt desert, and lower juniper-pinyon communities in San Juan County; Colorado and Arizona eastward to Texas and south to Mexico.

Lesquerella garrettii Payson. Perennial, cespitose, caudex simple or few- to several-branched, branches clothed with marcescent leaf-bases and scars; herbage pubescent with stellate hairs; stems 0.5-1.5 dm tall, decumbent-spreading to suberect, simple; basal leaves 1-3.5 (4) cm long, 0.2-0.7 cm wide, elliptic to obovate, differentiated into blade and petiole; cauline leaves 0.3-1.3 cm long, 0.1-0.4 cm wide; pedicels 3.5-7 mm long, straight or curved, spreading-ascending; sepals 4.5-6 mm long; petals 6-9 mm long, yellow, spatulate to obovate; silicles (excluding style) 3.5-4 mm long, short-stipitate, subglobose or obovoid, valves pubescent externally, glabrous within; styles 4-7 mm long; ovules 2-4 per locule.— Rocky sites at high elevations, from 2900 to 3350 m elevation in Salt Lake, Utah, and Wasatch counties; endemic. The type was collected in Big Cottonwood Canyon, Salt Lake County.

Lesquerella hemiphysaria Maguire. Perennial, cespitose, caudex simple or few-branched, branches more or less clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.3-1 (1.5) dm tall, decumbent-spreading or sometimes rarely erect; basal leaves 0.5-3.5 (5.5) cm long, 0.4-1 (1.5) cm wide, obovate to elliptic, differentiated into blade and petiole; cauline leaves 0.3-1.5 cm long, 0.2-0.5 cm wide; pedicels 3-7 mm long, spreading, ascending, or recurved, S-shaped or curved; sepals 4-7 mm long; petals 5-7 mm long, yellow, oblanceolate; silicles (excluding style) 3-7 mm long, sessile or substipitate, obcordate in outline, valves more or less pubescent externally, glabrous within; styles 3-6 mm long; seeds 4-8 per locule.

1. Silicles glabrous or nearly so; plants of the West Tavaputs Plateau .... *L. hemiphysaria* var. *lucens*
   Silicles uniformly pubescent throughout; plants of the Wasatch Plateau .... *L. hemiphysaria* var. *hemiphysaria*

Var. *hemiphysaria.* Meadows and ridgetops from 2600 to 3200 m elevation in Carbon, Emery, Sanpete and Sevier counties; endemic.

Var. *lucens* Welsh & Reveal var. nov. O *Lesquerella hemiphysaria* var. *hemiphysaria* differt in siliquis glabris vel fere glabris. Holotype: Utah, Carbon Co., 7 miles due northeast of Sunnyside, Range Creek Canyon, S. Welsh & K. Taylor 15139, 23 June 1977 (BRY, isotypes to be distributed). Paratype: Utah, Carbon Co., 6 miles north-northeast of Sunnyside, S. Welsh & K. Taylor 15122, 22 June 1977 (BRY). Sagebrush and woodland communities at 2700 to 2800 m on the West Tavaputs Plateau, Carbon Co.; endemic.

Lesquerella intermedia (S. Wats.) Heller. [*L. alpina* var. *intermedia* S. Wats.] Perennial, cespitose, caudex simple or few-branched, branches more or less clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.2-1.5 (2.5) dm tall, erect or ascending, simple; basal leaves 1-5 cm long, 0.1-0.2 cm wide, linear or only slightly expanded apically, inner usually involute, tapering gradually to base; cauline leaves 0.8-3.5 cm long, 0.1-0.3 cm wide; pedicels 4-12 mm long, spreading to ascending, straight or curved; sepals 2.8-6.5 mm long; petals 5.5-10.5 mm long, yellow, spatulate; silicles (excluding style) 4-7 mm long, sessile or substipitate, ellipsoid or ovoid, acute and somewhat flattened apically, pubescent externally, glabrous or pubescent within; styles (2) 3-4.5 mm long; seeds (4) 6-8 (10) per locule.— Aspen, mixed conifer, ponderosa pine, and pinyon-juniper communities, from 1525 to 2900 m elevation in Beaver, Emery, Garfield, Sevier, Washington, and Wayne counties; Arizona, New Mexico.

This taxon approaches *L. alpina* on the one hand and *L. rectipes* on the other. Definitive features to separate alpine phases of *L. intermedia* from *L. alpina* are subject to interpretation. Only arbitrary separation seems possible.

Lesquerella kingii S. Wats. Perennial, cespitose, caudex usually simple, densely clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.3-1.8 dm tall, decumbent to suberect, simple; basal leaves 1.5-4.5 (6) cm long, 0.4-2 cm wide, blade spatulate to oval, obovate or ovate, sharply differentiated from petiole; cauline leaves 0.5-2 cm long, 0.1-0.7 cm wide; pedicels 4-10 mm long or more, curved to straight or S-shaped, ascending to descending; sepals 4-8 mm long; petals 5.5-12 mm long, yellow, spatulate; siliques (excluding style) 3.5-9 mm long, sessile to substipitate, ellipsoid, compressed apically, valves pubescent externally, pubescent to glabrous within; styles 2-5 mm long; seeds 4-8 per locule.— Ponderosa pine and juniper-pinyon communities at low to moderate elevations in Garfield, Millard, Sevier, Tooele, and Washington counties; Nevada, California and Oregon.

Our material, which is not always distinguishable from *L. wardii*, belongs to var. *parvifolia* (Maguire & Holmgren) Welsh and Reveal, comb. nov., based on *Lesquerella occidentalis* var. *parvifolia* Maguire & Holmgren, Madroño 11: 179. 1951 [*L. latifolia* A. Nels.; *L. barnebyi* Maguire; *L. kingii* ssp. *latifolia* (A. Nels.) Rollins & Shaw]. The var. *cordiformis* (Rollins) Maguire & Holmgren is to be sought in the deserts of extreme western Utah.

Lesquerella ludoviciana (Nutt.) S. Wats. [*Myagrum argenteum* Pursh; *Alyssum ludovicianum* Nutt.; *L. argentea* (Pursh) MacMillan, not *L. argentea* (Schauer) S. Wats.] Perennial, loosely cespitose, caudex simple to many-branched, branches clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.7-3 (4) dm tall, ascending to erect or outer decumbent, simple; basal leaves 1-9 cm long, (0.1) 0.2-0.8 cm wide, spatulate to oblanceolate or appearing linear when folded; cauline leaves 1-6 cm long, 0.1-0.6 cm wide; pedicels 5-15 mm long or more, straight or curved, ascending to recurved; sepals 4-7 mm long; petals 5-10 mm long, yellow, oblanceolate to obovate; silicles (excluding style) 3-6 mm long, sessile or nearly so, subglobose or obovoid, valves pubescent externally and usually pubescent within; styles 3-5 mm long; seeds 2-8 per locule.— Pinyon-juniper, sagebrush, and upwards to spruce-fir woodlands, from 1370 to 2750 m elevation in Daggett, Duchesne, Garfield, Kane, and Uintah counties; Minnesota and Illinois westward to Montana, and southward to Nevada, Colorado, and Kansas.

Lesquerella multiceps Maguire. Perennial, cespitose, caudex simple or several- to many-branched, more or less clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.3-2 dm long, rarely more, prostrate to erect; basal leaves 1-6 cm long, 0.4-1.5 (2) cm wide, blades elliptic to obovate, differentiated from long slender petioles; cauline leaves 0.4-2 cm long, 0.1-0.5 cm wide; pedicels 3-10 mm long, S-shaped; sepals 4.3-7 mm long; petals 5-10 mm long, yellow, spatulate; silicles (excluding style) 3-5.5 mm long, sessile or nearly so, ovoid, valves pubescent externally, glabrous within; styles 3-6.5 rm long; ovules 2-4 per locule.— Ridges and upper slopes from 1830 to 3050 m elevation in Cache, Davis, and Rich counties; Idaho, Wyoming.

Lesquerella occidentalis S. Wats. Perennial, cespitose, caudex simple or few-branched, more or less clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.2-1.5 dm long, rarely more, prostrate, decumbent, ascending or erect, usually simple; basal leaves 0.5-8 cm long, 0.3-1.5 cm wide, blades spatulate to oval or obovate, differentiated from petioles; cauline leaves 0.4-1.5 cm long, 0.1-0.8 cm wide; pedicels 3-10 mm long or more, sigmoid or straight, ascending; sepals 4-7 mm long; petals 6-10 mm long, yellow, spatulate; silicles (excluding style) 4-6 mm long, ellipsoid, usually compressed at apex, valves pubescent externally and usually pubescent within; styles 2-5 mm long; seeds 2-8 per locule.— Limestone cliffs and talus slopes from 1525 to 3660 m elevation in Box Elder and Juab (Mt. Nebo) counties; Idaho and Utah to California and Oregon.

Our material belongs to var. *cinerascens* Maguire and Holmgren [*L. occidentalis* ssp. *cinerascens* (Maguire & Holmgren) Rollins & Shaw].

Lesquerella prostrata A. Nels. Perennial, cespitose, caudex simple or few-branched, branches more or less clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.3-1.5 dm tall, decumbent to ascending, simple; basal leaves 1-5 cm long, 0.5-1 (1.5) cm wide, blades deltate to hastate, more or less angular, differentiated from slender petioles; cauline leaves 0.4-1.5 cm long, 0.1-0.5 cm wide; pedicels 4-10 mm long, curved to straight or S-shaped, spreading; sepals 5-6 mm long; petals 5-9 mm long, yellow, spatulate; silicles (excluding style) 4-7 mm long, sessile or nearly so, ovoid to ellipsoid, not flattened apically, valves pubescent externally, glabrous or sparsely hairy within; styles 3-6 mm long; seeds 2-4 per locule. —Sagebrush community, especially on dry shaly slopes from 1830 to 2440 m elevation in Rich (and to be sought in Summit) County; Wyoming and Idaho.

Lesquerella rectipes Woot. & Standl. Perennial, loosely cespitose, caudex simple or few-branched, branches more or less clothed by marcescent leaf-bases; stems 0.4-4 dm tall or more, decumbent to ascending or erect, simple or branched; basal leaves 1-8 (10) cm long, 0.3-1.2 cm wide, oblanceolate to elliptic, entire or toothed, tapering gradually to base; cauline leaves 0.6-3 cm long, 0.2-1 cm wide; pedicels 4-10 mm long or more, straight or S-shaped, spreading to ascending or recurved; sepals 4-8 mm long; petals 6-10 mm long or more, yellow, spatulate to obovate; silicles (excluding style) 4-7 mm long, substipitate to subsessile, ovoid to ellipsoid, pubescent externally and glabrous or pubescent within; styles 2-7 mm long; seeds 4-8 per locule.— Pinyon-juniper, grasslands, warm desert shrub, and ponderosa pine communities from 1220 to 2440 m elevation in Carbon, Emery, Garfield, Grand, Kane, San Juan, Uintah, Washington and Wayne counties; Utah and Arizona eastward to Colorado and New Mexico.

This is the most common of the tall species of *Lesquerella* in southeastern Utah.

Lesquerella rubricundula Rollins. [*L. hitchcockii* ssp. *rubicundula* (Rollins) Maguire & Holmgren] Plants perennial, loosely cespitose, not matted, caudex simple or with few to several branches, branches clothed with marcescent leaf bases; herbage pubescent with stellate hairs; stems 0.1-0.5 dm tall, erect, simple; leaves mainly basal, 0.3-1.2 cm long, 0.1-0.2 cm wide, not differentiated into blade and petiole; pedicels 1-6 mm long, straight or curved, ascending; sepals 3.2-4.5 mm long; petals 4.5-7 mm long, yellow, spatulate; silicles (excluding style) 3-5 mm long, sessile to substipitate, ovoid, valves glabrous externally and within; styles

2.8-3.5 mm long; ovules 2-4 per locule.—Mixed conifer woodlands, on White and Pink limestone member of the Wasatch Formation from 2440 to 3050 m elevation in Garfield (type locality at Red Canyon) and Iron counties; endemic.

Lesquerella subumbellata Rollins. Perennial, cespitose, caudex several-branched, branches clothed with marcescent leaf bases and often with leaves as well; herbage pubescent with stellate hairs; stems 0.1-0.8 (1) dm tall, ascending to erect, simple; basal leaves 0.8-3 cm long, 0.2-0.6 (1) cm wide, at least outer and usually most of them obovate-spatulate, gradually tapering to petiole; cauline leaves 0.3-2 cm long, 0.1-0.4 cm wide; pedicels 2-5 mm long, straight or curved, ascending; sepals 3-4.5 mm long; petals 5-6 mm long, yellow, spatulate; silicles (excluding style) 3.5-5 mm long, subsessile, ellipsoid, valves pubescent externally; styles 1.5-2.5 mm long; seeds 2-6 per locule.—Pinyon-juniper and sagebrush communities from 1680 to 1980 m elevation in Duchesne and Uintah (type locaity 18 miles north of Vernal) counties; Colorado, Wyoming.

Rollins and Shaw (1973) place this taxon within the range of variation of *Lesquerella alpina*. That disposition ignores the basic continuity of *L. subumbellata*, and likewise denies the apparent relationship of *L. alpina* in quite another direction, i.e., with *L. intermedia*. The uniformly broad blades of basal leaves, although tenuous as a diagnostic feature, are on the order of other diagnostic features in this critical genus.

Lesquerella tenella A. Nels. [*L. gordonii* var. *sessilis* S. Wats.; *L. palmeri* of Utah references, not S. Wats.] Annual, herbage pubescent with stellate hairs; stems 1-5 dm tall or more, spreading-decumbent to erect, simple or branched; basal leaves 1.5-6 cm long, 0.2-1.5 cm wide, blades elliptic, sometimes toothed, differentiated from petiole; cauline leaves 0.4-4 cm long, 0.2-1 cm wide; pedicels 4-12 (18) mm long or more, S-shaped, spreading to recurved; sepals 3.5-7 mm long; petals 5-10 mm long, yellow to orange, orbicular to obovate; silicles (excluding style) 3.5-5 mm long, sessile to substipitate, globose to obovoid, valves pubescent externally and internally; styles 2-4.5 mm long; ovules 2-6 per locule.—Blackbrush, cresote brush, and Joshua tree communities at lower elevations in Washington County (the type of var. *sessilis* is from St. George); Nevada and California south to Mexico.

Lesquerella tumulosa (Barneby) Reveal. [*L. hitchcockii* ssp. *tumulosa* Barneby] Perennial, pulvinate-cespitose, densely matted, caudex many-branched, branches clothed with numerous marcescent leaves and leaf bases; herbage pubescent with stellate hairs; stems 0.1-0.4 dm tall, erect, simple; leaves mainly basal, 0.2-1 (1.5) cm long, (0.07) 0.1-0.15 (0.2) cm wide, not differentiated into blade and petiole; pedicels 2-5 mm long, straight or S-shaped, spreading to ascending; sepals 2.8-4 mm long; petals 5-7 mm long, yellow, spatulate; silicles (excluding style) 2.7-3.8 mm long, substipitate, ovoid, valves glabrous externally and internally; styles 1.9-2.7 mm long; ovules 2-4 per locule.—White, bare shale knolls (Winsor Member of the Carmel Formation) among scattered juniper in a *Bouteloua* grassland, Kane County; endemic.

This plant was included with *L. rubicundula* by Rollins and Shaw (1973), but is distinct morphologically, spatially, and substrate-wise from that taxon as noted by Reveal (Great Basin Nat. 30:94-98. 1970).

Lesquerella utahensis Rydb. Perennial, cespitose, caudex usually simple, more or less clothed with persistent leaf-bases; herbage pubescent with stellate hairs; stems 0.2-1.5 dm tall or more, decumbent to ascending or erect; basal leaves 1.2-6.5 cm long, 0.1-0.5 cm wide; pedicels 3-10 mm long, sigmoid or curved, ascending; sepals 4.5-5.7 (7) mm long; petals 6.5-9 mm long, yellow, spatulate; siliques (excluding style) 3.5-4.5 (6) mm long, substipitate to sessile, globose-ellipsoid, compressed contrary to partition, valves pubescent externally, glabrous internally; styles 4-5.5 (6.5) mm long; seeds 3-6 per locule.—Openings among spruce-fir woodlands from 2600 to 3350 m elevation in Duchesne, Salt Lake, Summit, Uintah, Utah (the type is from American Fork Canyon), and Wasatch counties; endemic.

Lesquerella wardii S. Wats. Perennial, caudex usually simple, clothed with marcescent leaf-bases; herbage pubescent with stellate hairs; stems 0.2-2 dm tall, rarely more, decumbent to ascending or erect, simple; basal leaves 1-4.5 (6) cm long, 0.3-1.5 (2) cm wide, blades deltoid to orbicular or elliptic, differentiated from slender petiole; pedicels 2-7 mm long, straight, curved, or S-shaped, ascending; sepals 4-6.3 (8) mm long; petals (5.5) 6-9 (11) mm long, yellow, spatulate; silicles (3.5) 4-6.8 (8) mm long, substipitate to sessile, ellipsoid or ovoid, not compressed apically, pubescent externally and usually so internally; styles (1) 2.2-4 (7) mm long; seeds 2-8 per locule.—Spruce-fir woodlands, meadows, pinyon-juniper, and desert shrub communities from 1830 to 3400 m elevation in Beaver, Garfield (type area is Aquarius Plateau), Iron, Kane, Millard, Piute, Sevier, and Washington counties.

Lesquerella wardii is most similar to the partially sympatric *L. kingii* var. *parvifolia* from which it is distinguished inter alia in the silicles being rounded, not compressed, apically.

LOBULARIA Desv.
Nom. Cons.

Plants annual or rarely biennial, pubescent with malpighian hairs, arising from taproots; leaves alternate, simple, entire, petiolate or sessile, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white, pink, or lavender; stamens 6, filaments lacking glandular processes; style short, stigmas capitate; fruit a silicle, about as broad as long, compressed parallel to septum, dehiscent, valves 1-nerved; seeds 1 per locule.

A European genus of 5 species.

Lobularia maritima (L.) Desv. [*Clypeola maritima* L.; *Alyssum maritimum* (L.) Lam.] Sweet Alyssum. Annual, stems spreading-decumbent or ascending to erect, usually much branched, 0.8-3 dm long or more; leaves linear-oblanceolate, 0.8-3 (4) cm long, 0.1-0.4 cm wide, strigose on both surfaces; pedicels spreading-ascending, 5-9 mm long; sepals 1-1.5 (2) mm long, green or purplish, pubescent; petals 2.5-4 mm long, white, pink or lavender, the blades obovate; silicles 2.5-3.5 mm long and about as broad, valves sparingly strigose; styles 0.3-0.6 mm long.—Ornamental border plant with sweetly scented flowers, escaping and occasionally persistent; introduced from Europe.

LUNARIA L.

Plants annual or biennial, pubescent with simple or with some forked hairs, arising from taproots; leaves usually alternate and basal, simple, dentate to lobed, petiolate, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, pink to lilac or blue or purplish; stamens 6, filaments lacking glandular processes; style elongate, persistent, stigma capitate, bilobed; fruit a stipitate silicle, about as broad as long, compressed parallel to septum, dehiscent, valves reticulately veined; seeds 3-5 per locule.

A small Eurasian genus of 2 or 3 species.

Lunaria annua L. Honesty; Moonwort; Satin-flower. Plants with one to several stems, these simple or branched, mostly 4-10 dm tall or more, pubescent with simple, and rarely with some forked, hairs; leaves 2.5-10 (15) cm long, 1.5-8 cm wide, rarely more, ovate to lance-ovate or cordate, dentate to lobed, pubescent with simple or rarely forked hairs; pedicels 10-22 mm long, spreading-ascending, pubescent; sepals 6-8 mm long, greenish or variously suffused, sparsely pubescent; petals 14-20 mm long, pink to lilac or blue to purplish, obovate; silicles 32-45 mm long, 25-35 mm wide, borne on stipes 7-12 mm long, much flattened, valves glabrous; styles 6-8 mm long. —Ornamental, cultivated for the showy flowers and distinctive fruiting inflorescences, occasionally escaping; introduced from Europe.

MALCOMIA (L.) R. Br.
Nom. Cons.

Plants pubescent with forked or 3-rayed hairs, annual, from taproots; leaves alternate and basal, simple, sinuate-dentate, cauline ones petiolate to sessile, not auriculate; flowers racemose, pedicels seldom subtended by bracts; sepals 4, tardily deciduous; petals 4, pink to lavender; stamens 6, filaments lacking glandular processes; style tapering, stigma oblique; fruit a silique, many times longer than broad, subterete, dehiscent, valves nerveless; seeds uniseriate.

About 30 species of Europe and Africa, with 2 or 3 species in North America as weeds.

Malcolmia africana R. Br. in Ait. Plants decumbent-ascending to erect, stems 0.3-4 dm tall, simple or branched almost throughout, pubescent with forked or 3-rayed hairs; leaves mainly basal to mainly cauline, 1.2-9 cm long, 0.3-2.3 cm wide, oblanceolate to elliptic, sinuate-dentate, petiolate to sessile, not auriculate; pedicels spreading, 1-2 mm long, pubescent; sepals 3.7-5.2 mm long, often reddish or purplish, pubescent; petals 6.2-9.5 mm long, pink to lavender, rounded apically, spreading; siliques 33-66 mm long, straight, pubescent; style up to 1 mm long, stigma oblique.—Roadsides, foothills, and other disturbed sites at lower elevations in Cache, Carbon, Emery, Garfield, Grand, Juab, Kane, Millard, Salt Lake, San Juan, Sevier, Tooele, Uintah, Utah, and Washington counties, and probably throughout the state; widespread throughout the Great Basin and adjacent areas of the western United States; adventive from Africa.

NASTURTIUM R. Br.

Plants glabrous perennials from subrhizomatous stolons; leaves alternate, simple or some pinnately compound, petiolate and auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white; stamens 6, filaments lacking glandular processes; styles stout, well developed, stigma capitate, bilobed; fruit a silique, several times longer than broad, oblong, somewhat compressed parallel to septum, the valves 1-nerved; seeds several to many, biseriate.

Perhaps 50 species of moist places in the temperate zones.

Nasturtium officinale R. Br. in Ait. [*Sisymbrium nasturtium-aquaticum* L.; *Rorippa nasturtium-aquaticum* (L.) Schinz & Thell.] Watercress. Plants submersed or emergent, succulent stems (0.3) 1-8 (10) dm long or more, glabrous; leaves 1-10 cm long, terminal lobe usually largest, falsely petiolate and narrowly auriculate-clasping basally; pedicels 5-13 (20) mm long, spreading to spreading-ascending, glabrous or pubescent; sepals 2-3 mm long, green or tips white, glabrous; petals 3-4.7 mm long, white, rarely with veins purplish, oblanceolate; siliques 10-18 (25) mm long, 1.8-2.4 mm wide; styles 0.7-1.2 mm long.—Seeps, springs, and sluggish streams, usually in flowing water at moderte elevations in Cache, Garfield, Grand, Iron, Millard, Salt Lake, San Juan, Summit, Utah, Wasatch, Washington, Wayne, and Weber counties, and probably throughout the state; widely established in North America; introduced from Europe.

Watercress is used as a salad plant.

PARRYA R. Br.

Plants perennial, glabrous, pubescent with stipitate-glandular hairs, arising from taproots and with simple to branched caudices; leaves mainly basal, simple, dentate, tapering basally, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, pink to lavender; stamens 6, filaments lacking glandular processes; styles stout, persistent, stigmas bilobed; fruit a silique, usually several times longer than broad, oblong, constricted between seeds, strongly compressed parallel to septum, valves 1-nerved; seeds 1 to several per locule.

An Asian and North American genus of perhaps 25 species.

Parrya rydbergii Botsch. [*P. platycarpa* Rydb., not Hook. f. & Thomas] Plants rosulate, low perennials, caudex clothed with marcescent leaf bases; stems scapose, 0.7-1.2 dm tall, 2-8 cm to base of raceme, herbage stipitate-glandular; leaves 3-10 cm long, 0.6-2 cm wide, oblanceolate to elliptic; flowers racemose, 3-7 (10); pedicels 4-20 mm long, stout, steeply ascending; sepals 7.2-9.3 mm long, purplish, stipitate-glandular or glabrous; petals 16-23 mm long, pink to lavender, cuneate-spatulate, emarginate; siliques 25-47 mm long, 3-3.5 mm wide, straight or curved, midnerve prominent, glabrous or stipitate-glandular; style 0.3-0.6

mm long, stigma deeply bilobed; seeds 1-4 per locule.—Talus slopes, krumholz communities, and alpina tundra sites in the Uinta Mountains from 3200 to 3720 m elevation in Daggett, Duchesne, Summit, and Uintah counties; endemic.

This is one of our most unique and attractive Utah endemic species, and one that may be worthy of cultivation if low-elevation cultivars could be developed.

PHYSARIA (Nutt.) A. Gray

Plants stellate pubescent perennials, arising from taproots; leaves mainly basal, cauline ones much reduced, alternate, simple, tapering basally or merely sessile, not auriculate; flowers racemose, pedicels straight, curved, sigmoid, spreading or descending, not subtended by bracts; sepals 4, deciduous; petals 4, yellow, rarely purple, rounded; stamens 6, filaments lacking glandular processes; style slender, stigma capitate; fruit a sessile, bladdery-inflated silicle, often broader than long, varying in outline, compressed (if at all) contrary to septum, valves veinless; seeds 2-6 per locule, biseriate.

A genus of perhaps 15 species restricted to western North America.

The diagnostic features used to segregate entities of this genus are mainly based on the shape of the mature silicle and the length of the style. These features are subject to variation within rather broad limits, and not all specimens will fit neatly into the following key. Immature specimens are particularly difficult to place, and strictly fruiting collections are often more readily definable than flowering collections.

Mulligan, G. A. 1967. Cytotaxonomy of *Physaria acutifolia*, *P. chambersii*, and *P. newberryi* (Cruciferae). Canad. J. Bot. 45:1887-1898.

Payson, E. B. 1918. Notes on certain Cruciferae. *Physaria*. Ann. Missouri Bot. Gard 5:143-147.

Rollins, R. C. 1939. The cruciferous genus *Physaria*. Rhodora 41:392-415.

Waite, S. B. 1973. A taxonomic revision of *Physaria* (Cruciferae) in Utah. Great Basin Nat. 33:31-36.

1. Styles 2-3 (4) mm long; valves of silicles sharply angled at maturity; plants of Grand, Kane, San Juan, and Washington counties .... *P. newberryi*
   Styles mostly 4-8 mm long or more; valves of silicles obtusely angled to rounded at maturity; distribution various 2

2(1). Basal leaves sinuate-dentate to lobed, sometimes with some entire; cauline leaves often toothed; plants endemic to Uintah Basin .... *P. grahamii*
   Basal leaves entire or rarely sinuate-dentate; cauline leaves entire; plants of broad distribution 3

3(2). Sinuses of silicles indented above and below, when immature equally rounded to apex and base; valves rounded, not angled at maturity; plants mainly of the Colorado River drainage system .... *P. acutifolia*
   Sinuses of silicles only slightly indented to rounded below, deeply indented above, when immature tapering to base and obcordate in outline; valves obtusely angled at maturity; plants mainly of Great Basin and valleys of Virgin River drainage system .... *P. chambersii*

Physaria acutifolia Rydb. Plants perennial, cespitose, caudex usually simple, clothed with marcescent leaf bases; stems 0.3-2 (2.5) dm long, decumbent to ascending or erect, simple; basal leaves 1.7-9.5 cm long, 0.7-3 cm wide, blade orbicular to ovate or obovate, less commonly lance-elliptic, entire, angular, or toothed; cauline leaves greatly reduced; pedicels mostly 7-16 mm long, ascending to descending; sepals 5.2-8.7 mm long; petals 7.5-12.5 mm long, yellow or purple, spatulate; silicles bladdery-inflated, sinuses indented above and somewhat less so below, valves 7-15 mm long in fruit, surface rounded in cross-section, papery to membranous; styles 3.8-7 mm long. —Desert shrub, pinyon-juniper, sagebrush, and oak communities from 1220 to 2440 m elevation in Carbon, Daggett, Duchesne, Emery, Garfield, Grand, Kane, San Juan, Sevier, Uintah, and Wayne counties; Idaho and Utah eastward to Wyoming, Colorado, and New Mexico.

This very critical species contacts *P. chambersii* to the west where apparent intermediates are known; a similar situation occurs southward involving *P. newberryi*. Two varieties are known.

1. Flowers clear yellow, rarely fading purplish; silicles definitely indented below; plants widespread .... *P. acutifolia* var. *acutifolia*
   Flowers purple or tinged purple; silicles only slightly indented below; plants known only from the Book Cliffs area of Grand County .... *P. acutifolia* var. *purpurea*

Var. ***acutifolia***. [*P. didymocarpa* var. *australis* Payson; *P. australis* (Payson) Rollins] Plants widespread, our common phase.

Var. ***purpurea*** Welsh & Reveal, var. nov. Plantis similis *P. acutifolia* var. *acutifolia* sed petalis purpureis et siliculis pauci indentibus inferioribus. Type: Grand County, Utah, Sego Canyon, 5 miles north of Thompson, 1 May 1968, S. *L. Welsh 6902*. Holotypus, BRY. Paratype: Utah, Grand County, about 3 miles north of Thompson, 5 May 1971, S. *L. Welsh 10966* (BRY). Known only from the type locality.

Physaria chambersii Rollins. [*P. chambersii* var. *membranacea* Rollins] Plants perennial, cespitose, the caudex usually simple, clothed with marcescent leaf bases; stems 0.3-2.5 dm long, decumbent to ascending or erect, simple; basal leaves 1-7.5 (13) cm long, 0.3-3.5 cm wide, blade orbicular to ovate, obovate, elliptic or oblanceolate, entire, angular or toothed; cauline leaves greatly reduced; pedicels mostly 4-18 mm long, ascending to descending; sepals 6-7.2 mm long; petals 8-13 mm long, yellow, spatulate; silicles bladdery-inflated, upper sinus deeply indented, lower shallow or lacking, valves 11-17 mm long in mature fruit, surface roughly angled at edges, angles obtuse, papery to membranous; styles 4-8 mm long. —Desert shrub, sagebrush, oak-juniper, pinyon-juniper, aspen-mixed conifer, ponderosa pine, and spruce-fir communities from 1200 to 2900 m elevation in Beaver, Emery, Garfield, Iron, Juab, Kane, Millard, Piute, Sanpete, Sevier, Summit, Tooele, Utah, and Washington counties; Arizona and Utah west to California and Oregon.

Physaria grahamii Morton. Plants perennial, cespitose, caudex simple, clothed with marcescent leaf bases; stems 0.5-1.5 dm long, ascending to erect, simple; basal leaves 2-15 cm long, 0.8-5 cm wide, blade oblanceolate to spatulate, toothed to pinnatifid; cauline leaves often toothed, much reduced; pedicels 6-20 mm long, ascending; sepals 4.5-5 mm long; petals about 6.5 mm long, yellow, spatulate; siliques strongly inflated, cordate, to 9 mm long and 10 mm wide; styles 3.5-7 mm long. Duchesne, Uintah, and Grand Cos.; Colorado.

This distinctive taxon is still only poorly understood. We have seen only the holotype (Chandler Canyon, 3 Aug 1935, *Graham 9976*, US), plus fruiting material gathered in August 1976 (*Welsh et al. 14414*, BRY). A second collection made by Welsh (Welsh & Higgins 6239, BRY) from Garfield County, Colorado, seems to belong to this taxon. The species appears to be endemic to soils derived from the Green River Shale Formation in the southern portion of the Uinta Basin and along the escarpments south of the Basin proper.

Physaria newberryi A. Gray. [*Coulterina newberryi* (A. Gray) Kuntze; *P. didymocarpa* var. *newberryi* (A. Gray) M. E. Jones] Plants perennial, cespitose, caudex simple, clothed with marcescent leaf bases; stems 0.4-2.2 dm long, decumbent to ascending or erect; basal leaves 2-7.5 cm long, 0.8-4 cm wide, blade obovate to orbicular, ovate, or spatulate, angled, indistinctly toothed or more commonly entire; cauline leaves much reduced, entire; pedicels 5-17 mm long, ascending to descending; sepals 6-8.5 mm long; petals 6.5-12 mm long, yellow, spatulate; silicles bladdery-inflated, upper sinus deeply indented, lower sinus shallow or lacking, valves 8-11 mm long or more in fruit, sharply angled at margins, papery; styles 2-3.5 mm long. —Warm desert shrub upwards to ponderosa pine communities from 1200 to 2000 m in Grand, Kane, San Juan and Washington counties; Arizona and New Mexico.

Where this species contacts either *P. chambersii* or *P. acutifolia* there are transitional specimens. Style length forms a continuum from one entity to another, and errors in determination are possible, especially in material which lack mature fruits.

RAPHANUS L.

Plants pubescent with simple hairs, annuals, from tuberous taproots; leaves alternate and basal, simple, lyrate-pinnatifid, cauline ones petiolate to subsessile, not auriculate; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white or pink to lavender; stamens 6, filaments lacking glandular processes; styles apical on a tapering sterile beak, stigma minute, bilobed; fruit a silique, many times longer than broad, terete, indehiscent, breaking irregularly at maturity into segments, valves several-grooved; seeds uniseriate.

About 6 Eurasian species.

Raphanus sativus L. Radish. Plants erect, stems mostly 4-10 dm tall, simple or more commonly branched, more or less hispid with simple hairs; leaves basal and cauline, mostly 2-18 cm long, 0.5-6.5 cm wide, lyrate-pinnatifid, hispid, cauline ones reduced upwardly; pedicels 10-20 mm long or more, spreading to ascending; sepals 7-9 mm long, green to reddish or purplish, glabrous; petals 12-20 mm long, white to pink or lavender; siliques 30-60 mm long, 5-10 mm wide, beak 10-25 mm long. —Cultivated for the edible roots, rarely escaping but usually not persisting; introduced from Europe.

The yellow-flowered species, *R. raphanistrum* L., is an occasional weed which is to be expected in the state.

RORIPPA Scop.

Plants glabrous to hirsute with simple hairs, annual, biennial or perennial, from taproots or rhizomes; leaves alternate and basal, lyrate-pinnatifid, sinuately toothed, lobed, or uppermost subentire, petiolate to sessile, auriculate in some; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow, fading pinkish in some, truncate to rounded apically; stamens 6, filaments lacking glandular processes; style prominent to almost lacking, stigma capitate; fruit a sessile silique or silicle from one to several times longer than broad, terete or somewhat flattened; seeds several to numerous, mostly biseriate.

A genus of perhaps 40 species on all major continents, but mainly in the northern temperate regions of the world.

Stuckey, R. L. 1972. Taxonomy and distribution of the genus *Rorippa* (Cruciferae) in North America. Sida 4:279-430.

1. Plants perennial, with creeping rhizomes; petals 2.5-5 mm long 2
   Plants annual or biennial, rarely perennial, from taproots; petals 0.7-2.5 (3) mm long 3

2(1). Plants 3-9 dm tall; sepals 1-2 mm long; fruits globose, usually seedless; introduced weeds of cultivated lands .... *R. austriaca*
   Plants 1-3 dm tall; sepals 2-4 mm long; fruit ovoid to oblong, bearing seeds; indigenous plants of saline valley bottoms .... *R. sinuata*

3(1). Siliques globose, 1-1.3 times longer than broad; partition circular in outline .... *R. sphaerocarpa*
   Siliques cylindroid or tapering at the apex, 2-5 times longer than wide or more; partition oblong to triangular in outline 4

4(3). Plants prostrate to decumbent, stems 2 dm long or less; siliques tapering to apex, minutely papillose .... *R. tenerrima*

Plants prostrate to decumbent or erect, stems often over 2 dm long; siliques cylindroid or tapering to apex, smooth 5

5(4). Plants erect, stems mostly 3-10 dm long; pedicels usually as long as fruit, mostly 4-12 mm long .... *R. islandica*

Plants prostrate, decumbent, ascending, or erect, mostly 2-5 dm tall; pedicels usually shorter than fruit, mostly 2-4 mm long .... *R. curvipes*

Rorippa austriaca (Crantz) Besser. [*Nasturtium austriacum* Crantz; *Radicula austriaca* (Crantz) Small] Austrian field-cress. Perennial, from thickened rhizomes, stems 3-9 dm tall, erect, slender, finely puberulent; leaves 3-6 cm long, oblong to oblong-ovate, unequally serrate, glabrous, narrowed to a petiolelike auriculate base; racemes 7-12 cm long, in terminal panicles; pedicels 4-10 mm long in fruit, spreading-ascending; sepals 1-2 mm long; petals 3-15 mm long, yellow; silicles subglobose, 1.5-3 mm long. —Occasional to rare weed of cultivated places, reported for south-central Utah by Stuckey (1972).

Rorippa curvipes Greene. Annual or short-lived perennial, arising from taproots, stems (1) 2-5 dm long, prostrate to decumbent, ascending or erect, glabrous; leaves (2) 4-8 (12) cm long, 0.3-1.5 cm wide, oblong, obovate, spatulate or oblanceolate, entire, crenate, irregularly serrate, or lower ones pinnatifid, petiolate to sessile, often auriculate; racemes 4-15 cm long, in axillary and terminal racemes; pedicels mostly 2-5 mm long in fruit, spreading to ascending or descending; sepals 0.8-1.7 mm long; petals 0.5-2.8 mm long, yellow, rarely fading pinkish; silicles 1.8-8.7 mm long, 0.6-2.3 mm wide; style 0.2-1.3 mm long. —Moist sites from low to high elevation throughout much of Utah; western North America from southern Canada to Arizona and New Mexico.

Three more or less distinct varieties are recognized.

1. Petals 1.2-2.8 mm long, longer than sepals; siliques usually acute; plants prostrate to decumbent .... *R. curvipes* var. *alpina*

Petals mostly 0.5-1.5 mm long, about as long as or shorter than sepals; siliques acute or obtuse; plants prostrate to decumbent or erect 2

2(1). Siliques 1.4-5 mm long, acute to somewhat obtuse; petals 0.5-1 (1.3) mm long *R. curvipes* var. *curvipes*

Siliques 3.5-8 mm long or more, obtuse apically; petals 1-1.5 mm long .... *R. curvipes* var. *integra*

Var. *alpina* (S. Wats.) Stuckey. [*Nasturtium obtusum* var. *alpinum* S. Wats.; *R. obtusa* var. *alpina* (S. Wats.) Britton; *R. alpina* (S. Wats.) Rydb.; *Radicula alpina* (S. Wats.) Greene] Bogs and seeps from 1980 to 3050 m elevation in Cache, Duchesne, Garfield, Summit (type from head of Bear River Canyon), and Utah counties; Idaho, Wyoming, and Colorado.

Var. *curvipes*. [*Cardamine palustris* var. *jonesii* Kuntze; *R. underwoodii* Rydb.; *Radicula curvipes* (Greene) Greene; *Radicula underwoodii* (Rydb.) Heller; *Rorippa obtusa* and *Rorippa curvisiliqua* of Utah authors] Ponds, streams, and seep margins from 1370 to 2440 m elevation in Garfield, Grand, Kane, Piute, Salt Lake (type of var. *jonesii* from City Creek Canyon), Sanpete, Sevier, Utah, Wasatch, and Washington counties; Alberta and Saskatchewan east to Wisconsin and south to California, Arizona, New Mexico, and Kansas.

Var. *integra* (Rydb.) Stuckey. [*R. integra* Rydb.; *Radicula integra* (Rydb.) Heller; *Rorippa obtusa* var. *integra* (Rydb.) Marie-Victorin] Stream banks and beaches from 2440 to 3050 m elevation in Box Elder, Piute, Summit, Utah, and Wasatch (the probable type area) counties; Alberta south to California and east to Montana and Wyoming.

Rorippa islandica (Oeder) Borbas. Annual or biennial, arising from taproots, stems 3-10 dm tall, erect, glabrous or pubescent; leaves mostly 2-10 cm long, 0.6-2.5 cm wide, more or less pinnatifid, or cauline ones merely toothed, petiolate to sessile and more or less auriculate; racemes 3-10 cm long or more, in axillary and terminal racemes; pedicels mostly 4-10 mm long in fruit, ascending to spreading or descending; sepals 1.2-2.5 mm long; petals 0.8-3.5 mm long, yellow, fading pinkish or purplish; siliques 3-8 mm long, rarely more, 2-3 mm wide, valves glabrous; styles 0.2-1.2 mm long. —Lake shores, stream banks, springs, and seeps, mostly in northern Utah; widespread throughout the Northern Hemisphere.

Worldwide, or even within North America, this species is exceedingly complex. We have selected a conservative approach to the species, prefering to maintain *R. palustris* (L.) Besser [*Sisymbrium amphibium* var. *palustre* L.; *Sisymbrium palustre* (L.) Pollich; *Radicula palustris* (L.) Moench; *Nasturtium palustre* (L.) DC.] within the broad definition of *R. islandica* [*Sisymbrium islandicum* Oeder], and thereby differing from the recent treatment of the species complex in North America by Stuckey (1972). Within the North American populations, Stuckey recognizes several subspecies and varieties, denoting a bewildering array of morphological and geographically reinforced infraspecific variation. In Utah, we have only 2 of the 11 entities he recognizes.

1. Leaves glabrous beneath; stems glabrous or pubescent only at base .... *R. islandica* var. *glabra*
   Leaves hairy beneath; stems pubescent usually to apex .... *R. islandica* var. *hispida*

Var. ***glabra*** (O. E. Schulz) Welsh & Reveal, comb. nov., based on *Nasturtium palustre* var. *glabrum* O. E. Schulz, Symb. Antill. 3:516. 1903. [*Radicula glabra* (O. E. Schulz) Britton; *R. palustris* ssp. *glabra* (O. E. Schulz) Stuckey] Moist places in Garfield and Utah counties; Alberta south to New Mexico, with a disjunct series of populations on Cuba (the type area).

Var. ***hispida*** (Desv.) Butters & Abbe. [*Brachylobus hispidus* Desv.; *Sismybrium hispidum* (Desv.) Poir.; *Nasturtium hispidum* (Desv.) DC.; *N. palustre* var. *hispidum* (Desv.) A. Gray; *Radicula hispida* (Desv.) Britton; *Radicula palustris* var. *hispida* (Desv.) B. L. Robinson; *Rorippa palustris* ssp. *hispida* (Desv.) Jonsell] Moist sites from1370 to 2600 m elevation in Cache, Duchesne, Grand, Salt Lake, Summit, Utah, and Weber counties; widespread in North America.

Rorippa sinuata (Nutt.) A. S. Hitchc. [*Nasturtium sinuatum* Nutt. ex Torr. & Gray; *Radicula sinuata* (Nutt.) Greene] Perennial, arising from a slender rhizome, stems 0.8-5 dm long, often more or less decumbent, glabrous to minutely hairy; leaves (1) 2-8 cm long, oblong in outline, pinnatifid, petiolate to sessile and somewhat auriculate; racemes 3-15 (25) cm long, in axillary and terminal racemes; pedicels 5-11 mm long in fruit, ascending to recurved; sepals 2.7-4.5 mm long; petals 3.5-5.5 mm long, yellow, fading light yellow; siliques 5-12 mm long, about 1.5 mm wide, glabrous to roughened, narrowed to a style; styles 1-2.5 mm long.—Stream sides and other moist sites at lower elevations, not definitely known from Utah but reported from all of the surrounding states.

Rorippa sphaerocarpa (A. Gray) Britton. [*Nasturtium sphaerocarpum* A. Gray; *N. obtusum* var. *sphaerocarpum* (A. Gray) Wats. ex Allen; *Radicula sphaerocarpa* (A. Gray) Greene; *Radicula obtusa* var. *sphaerocarpa* (A. Gray) B. L. Robinson; *Rorippa obtusa* var. *sphaerocarpa* (A. Gray) Cory] Annual, arising from taproots, stems 1-4 dm long, decumbent to erect, sparingly hirsute below; leaves 3-10 cm long, 0.3-1.5 (3) cm wide, entire, crenate, serrate or pinnatifid; racemes 2-10 cm long, in axillary and terminal racemes; pedicels 1.5-4.2 mm long, ascending to recurved, often secund; sepals 0.7-1.3 mm long; petals 0.6-1.2 mm long, yellow, fading pinkish; siliques subglobose, 1-2.5 mm long and as wide or 1-1.3 times longer than broad; styles 0.4-0.7 mm long. —Moist sites at lower elevations in Garfield and Utah counties where evidently rare; Arizona and New Mexico northward to Wyoming.

This species approaches both *R. curvipes* and *R. islandica* var. *hispida*. Despite the apparent convergences, *R. sphaerocarpa* appears to exist as a functional entity and not just as an extreme morphological phase of either of the two taxa it approaches.

Rorippa tenerrima Greene [*Radicula tenerrima* (Greene) Greene] Annual, arising from taproots, the stems 0.4-2 dm long, decumbent to prostrate, glabrous; leaves 1-5 (8) cm long, 0.5-1.5 cm wide, lyrate-pinnatifid to subentire; racemes 2-10 cm long, in axillary and terminal racemes; pedicels 1-3 (4) mm long, ascending to spreading; sepals 0.7-1.2 mm long; petals 0.6-0.8 mm long, yellow; siliques 3-8 mm long, 0.8-2 mm wide, tapering to apex; styles 0.3-1 mm long. —Marshy sites at lower to mid elevations in Cache, Garfield, Kane, Iron, Salt Lake, Sevier, and Washington counties; Washington eastward to North Dakota and southward to Mexico.

SCHOENCRAMBE Greene

Plants glabrous, perennial, arising from a caudex and creeping rhizome; leaves alternate and some often basal, pinnatifid below, becoming entire above or all entire, petiolate to sessile, not auriculate; flowers racemose, the pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow; stamens 6, filaments lacking glandular processes; style almost lacking, stigma expanded, bilobed; fruit a sessile silique, many times longer than broad, terete, valves indistinctly 1-nerved; seeds uniseriate.

A western American genus of 2 species.

Schoencrambe linifolia (Nutt.) Greene. [*Nasturtium linifolium* Nutt.; *N. pumilum* Nutt., not St. Hilaire; *Sisymbrium linifolium* (Nutt.) Nutt ex Torr. & Gray; *Sisymbrium pygmaeum* Nutt. ex Torr. & Gray; *Erysimum glaberrimum* Hook. & Arn.; *Schoencrambe pygmaea* (Nutt.) Greene; *Schoencrambe pinnata* Greene; *Schoencrambe decumbens* Rydb.; *Schoencrambe linifolia* var. *pinnata* (Greene) A. Nels. in Coult. & Nels.; *Sisymbrium decumbens* (Rydb.) Blankinship; *Sisymbrium linifolium* var. *pinnatum* (Greene) O. E. Schulz; *Sisymbrium linifolium* var. *decumbens* (Rydb.) O. E. Schulz] Perennial, glabrous and usually glaucous, arising from a simple or more usually branched caudex, this from a creeping, deeply placed rhizome, stems (1.5) 2-9 dm tall, erect or less commonly ascending to decumbent, simple or branched; leaves 1.3-9.3 cm long, 0.1-2.5 cm wide, entire to deeply pinnatifid, basal ones often deciduous by midanthesis; pedicels 2-9 (10) mm long in fruit, ascending to spreading; sepals 4.3-6 mm long, yellowish; petals 7.5-11 mm long, yellow, spreading; siliques 25-65 (75) mm long, 0.8-1.2 mm wide, terete, sessile, erect or ascending; styles 0.3-0.6 mm long. —Salt desert shrub, sagebrush, and pinyon-juniper communities in Carbon, Daggett, Duchesne, Emery, Garfield (probable type location of *Schoencrambe pinnata*), Grand, Kane, Sanpete, Sevier, Summit, Uintah, Wasatch, and Wayne counties, and probably elsewhere; British Columbia east to Montana and south to Nevada and New Mexico.

The indecision as to the generic position of this plant is indicated by the numerous generic names associated with it. The plants simulate *Sisymbrium* in a broad sense but do not show apparent relationship with the introduced annual or biennial weedy species of that genus. It seems best to place this plant within its own genus even though the principle diagnostic features involve vegetative instead of floral characteristics.

SISYMBRIUM L.

Plants glabrous or hirsute annuals or rarely biennials, arising from taproots; leaves alternate and basal, variously lobed to entire, lower ones usually pinnatifid, reduced upwards, petiolate to sessile, not auriculate; flowers racemose, pedicels spreading to erect, not subtended by bracts; sepals 4, deciduous; petals 4, yellow; stamens 6, filaments lacking glandular processes; styles almost lacking, stigma bilobed; fruit a sessile silique many times longer than broad, linear to tapering, terete, valves usually 3-nerved; seeds several to many, uniseriate.

A complex genus of perhaps 75 species in temperate regions of the Old World and South America.

1. Leaves strongly dimorphic, lower lyrate-pinnatifid, uppermost with linear-filiform lobes; pedicels ascending, siliques 50-90 mm long, spreading-ascending to erect, not appressed; petals 6.3-8.5 mm long .... *P. altissimum*
Leaves not dimorphic, upper and lower lobed about same; pedicels ascending to erect, siliques 10-45 mm long, erect or ascending, appressed or not; petals 2-4 mm long 2

2(1). Siliques and pedicels ascending to spreading, not appressed to rachis, siliques (20) 25-45 mm long .... *S. irio*
Siliques and pedicels appressed-erect, siliques 10-15 mm long .... *S. officinale*

Sisymbrium altissimum L. [*Norta altissima* Britton] Jim Hill Mustard; Tumbling Mustard. Annual, stems 2.5-10 dm tall or more, sparingly to densely hirsute near base, usually glabrous above; leaves 1-20 cm long or more, petiolate, lower ones pinnatifid or merely lobed, becoming pinnatifid into line-filiform segments upwardly; pedicels 4-10 mm long, stout, almost or quite as thick as the silique, ascending to spreading; sepals 3.6-5 mm long, often yellowish; petals 6.3-8.5 mm long, yellow, fading white, obovate to spatulate, spreading; siliques 50-90 mm long, 1-1.5 mm wide, terete, spreading to ascending, valves evidently 3-nerved. —Usually in open disturbed sites at lower and middle elevations in Cache, Davis, Duchesne, Emery, Iron, Juab, Kane, Millard, Piute, Salt Lake, San Juan, Tooele, Utah, Wasatch, Washington, Wayne, and Weber counties, and probably cosmopolitan; widespread in North America; adventive from Europe.

Sisymbrium irio L [*Norta irio* (L.) Britton] Annual, stems 2-8 dm tall, erect, glabrous; leaves 1.5-10 (20) cm long, runcinate-pinnatifid to pinnatifid, reduced upwardly; pedicels 6-10 mm long, slender, ascending; sepals 2-2.5 (3) mm long, greenish or yellowish; petals 3-4 mm long, yellow, oblanceolate, spreading-ascending; siliques (20) 25-45 mm long, 0.8-1 mm wide, ascending. —Weed of dry sites in Beaver and Washington counties where locally common; California to Arizona; adventive from Europe.

Sisymbrium officinale (L.) Scop. [*Erysimum officinale* L.] Hedge Mustard. Annual, stems 2.5-8 dm tall or more, hispid-hirsute throughout; leaves 1.5-20 cm long or more, lyrate-pinnatifid to pinnatifid, not especially dimorphic, upper ones merely reduced; pedicels 2-3 mm long, stout, erect, tip about as thick as the silique; sepals 1.5-2.2 mm long, green or yellow; petals 3-4 mm long, yellow, fading white, narrowly oblanceolate, ascending; siliques 8-15 mm long, appressed-erect, tapering to beaklike tip, valves 3-nerved. —Uncommon weedy plant of disturbed sites in Utah County and to be expected elsewhere; widespread in North America; adventive from Europe.

SMELOWSKIA C. A. Meyer

Plants pubescent perennials, pulvinately cespitose, arising from a branching caudex, pubescence with branched and often with some simple hairs; leaves alternate or chiefly basal, usually pinnatifid, petiolate to sessile, not auriculate; flowers subcorymbose to racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white, rarely purplish; stamens 6, filaments lacking glandular processes; styles prominent, stigma expanded; fruit a silique, 3- to several times longer than broad, subterete or compressed, valves 1-nerved; seeds few to several per locule.

A genus of perhaps four species of Asia and North America. *Smelowskia holmgrenii* Rollins clearly does not belong to this genus, and this Nevada endemic probably ought to be placed in its own monotypic genus.

Drury, W. H., and R. C. Rollins. 1952. The North American representatives of *Smelowskia*. Rhodora 54:85-119.

Smelowskia calycina C. A. Meyer. Plants perennial, cespitose, with short to elongate caudex branches, these clothed with marcescent leaf bases; stems 0.4-2 dm tall, pubescent with short, branched and long, simple or branched hairs; basal leaves 0.5-5 cm long, 0.4-1.6 cm wide, pinnately divided; cauline leaves reduced upwardly; pedicels mostly 3-8 mm long in fruit, ascending to spreading-ascending, pubescent; sepals 2-3.2 mm long, often tinged purplish, pubescent; petals 3-8 mm long, white to cream or tinged pink to lavender, ovate, spreading; siliques 5-9 mm long, slightly flattened parallel to the septum or terete; styles 0.2-1 mm long; seeds 6-10. —Alpine tundra from 2900 to 3900 m elevation in Beaver, Daggett, Duchesne, Grand, Iron, Piute, Salt Lake, Uintah, and Utah counties; Alaska Yukon and Northwest Territories south to Nevada, Utah, and Colorado. Our material is var. *americana* (Regel & Herd.) Drury & Rollins [*Hutchinsia calycina* var. *americana* Regel & Herd.; S. *americana* (Regel & Herd.) Rydb.; S. *lineariloba* Rydb.; S. *lineariloba* f. *virescens* O. E. Schulz].

STANLEYA L.

Perennial, glabrous to simple pubescent herbs or subshrubs, arising from taproots or caudices; leaves alternate and basal, pinnatifid to entire, petiolate to sessile, auriculate in some; flowers showy, racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, yellow to greenish-yellow; stamens 6, filaments lacking glandular processes, long-exserted; styles lacking to prominent, stigma small; fruit a long-stipitate silique, linear, terete to compressed, valves 1- or more-nerved; seeds numerous, uniseriate.

A western North American genus of seven species.

Rollins, R. C. 1939. The cruciferaceous genus *Stanleya*. Lloydia 2:109-127.

1. Middle and upper cauline leaves sessile, auriculate; leaves all entire; petal-claw glabrous on both surfaces .... S. *viridiflora*
   Middle and upper cauline leaves petiolate to subsessile, not auriculate; leaves various; petal-claw pubescent on the inner or outer surfaces 2

2(1). Leaves entire or merely toothed, basal ones ovate to elliptic, cauline ones ovate to lanceolate or oblanceolate; plants of east-central and northeastern Utah .... S. *integrifolia*
   Leaves, at least some, pinnatifid, only upper ones entire and usually lanceolate to lance-linear; distribution various 3

3(2). Plants woody at base, caudex well developed; blades of petals mostly 1-3 mm wide; our most common and widespread species of the genus .... S. *pinnata*
   Plants herbaceous, caudex not developed; blades of petals 3-6 mm wide or more; an uncommon to rare plant of southeastern Utah .... S. *albescens*

Stanleya albescens M. E. Jones. Biennial, caudex neither woody nor well developed; stems 2.5-10 dm tall, glabrous and glaucous, simple or branched; leaves mostly 5-15 cm long, 1-5 cm wide, lyrate-pinnatifid or upper ones reduced in size and subentire to entire, glabrous and glaucous; pedicels mostly 5-10 mm long, spreading, glabrous; sepals 10-15 mm long, white with green tips, glabrous, reflexed; petals 10-16 mm long, blade 3-6 mm wide or more, claw hairy within; siliques 30-60 mm long, 1.5-2.5 mm wide, subterete, stipes 10-15 mm long. —Semidesert shrublands upwards to pinyon-juniper woodlands, to be expected in Grand or San Juan counties, not presently known from the state; Colorado and Arizona.

Stanleya integrifolia James. [S. *pinnatifida* var. *integrifolia* (James) B. L. Robinson; S. *glauca* var. *latifolia* Cockerell; S. *pinnata* var. *integrifolia* (James) Rollins] Perennial, caudex well developed and more or less woody; stems 2.5-9 dm tall or more, sparingly hairy, glaucous, simple or branched; leaves 0.8-12.3 cm long, 0.3-3.5 cm wide, elliptic to ovate or lanceolate, all entire or lower ones merely toothed, puberulent, glaucous; sepals mostly 9-19 mm long, yellowish, reflexed, glabrous; petals 10.5-15.5 mm long, blade 1.4-2.6 mm wide, claw hairy within; siliques 33-75 mm long, 1.2-1.8 mm wide, subterete, stipes 10-25 mm long. —Clay soils in desert shrub and pinyon-juniper communities from 1530 to 2000 m elevation in Daggett, Duchesne, Emery, and Uintah counties; Utah and Wyoming eastward to Kansas.

Our material is distinctive and about equivalent in diagnostic features found among the other species of *Stanleya* in Utah.

Stanleya pinnata (Pursh) Britton. [*Cleome pinnata* Pursh; S. *pinnatifida* Nutt.; S. *heterophylla* Nutt. ex Torr. & Gray; S. *fruticosa* Nutt.; S. *arcuata* Rydb.; S. *canescens* Rydb.; S. *glauca* Rydb.] Prince's Plume. Perennial, caudex well developed and slightly to very woody; stems (2.5) 3.5-12 (15) dm tall or more, glabrous to pilose, glaucous, simple or branched; leaves mostly 5-18 cm long, 2-5 cm wide or more, lanceolate to elliptic in outline, pinnatifid or upper usually entire and narrowly lanceolate to elliptic, not auriculate, glabrous or sparsely pilose; pedicels 4-13 mm long, spreading; sepals 11-22 mm long, yellowish, reflexed, glabrous; petals 11-17 mm long, blade 1-3.8 mm wide, claw hairy within; siliques (30) 35-70 (80) mm long, 1.2-2 mm wide, subterete to flattened, stipes 12-24 mm long, puberulent at base. —Seleniferous soils derived from shales, mudstones, and siltstones in many geological formations, from 850 to 2900 m elevation in Beaver, Box Elder, Carbon, Emery, Garfield, Grand, Iron, Juab, Kane, Millard, San Juan, Sanpete, Sevier, Uintah, Utah, Washington, and Wayne counties; Idaho east to North Dakota south to California, Arizona, and New Mexico.

This plant is a primary indicator of the poisonous element selenium, because the plant is common in such soils. Our material belongs to var. *pinnata*, but the var. *gibberosa* Rollins, known from Uinta County, Wyoming, is to be sought in Summit County, Utah. Its leaves are all bipinnate. The var. *inyoensis* (Munz & Roos) Reveal may be encountered in Washington County; it differs from var. *pinnata* in being a woody subshrub.

Stanleya viridiflora Nutt. ex Torr. & Gray. [S. *collina* M. E. Jones] Desert Plume. Perennial, caudex simple or branched, somewhat woody at base; stems 3-12 dm tall or more, glabrous and glaucous, simple or branched; leaves 7-30 cm long, basal ones 1.8-8.7 cm wide, petiolate, blades united or somewhat runcinate-pinnatifid, upper ones entire, sessile and auriculate, glabrous; pedicels mostly 6-12 mm long, spreading; sepals 11-20 mm long, yellow, reflexed, glabrous; petals 10-19 mm long, blade 0.8-1.5 (3) mm wide, not much wider than glabrous claw; siliques 35-70 mm long, subterete, stipe 14-25 mm long. —Gypsiferous or clay soils in sagebrush and pinyon-juniper communities from 1680 to 2450 m elevation in Duchesne, Emery, Salt Lake (?), Summit, Uintah, and Wayne counties; Idaho and Wyoming southwestwardly to Nevada and Oregon.

STREPTANTHELLA Rydb.

Plants glabrous, annual or winter annual, arising from taproots; leaves alternate, entire to shallowly dentate, tapering to base, not auriculate; flowers racemose, pedicels spreading-recurved to recurved, not subtended by bracts; sepals 4, deciduous; petals 4, white or purplish; stamens 6, the filaments lacking glandular processes; style obsolete, small capitate stigma borne atop a beaklike extension of fruit; fruit a subsessile, slender silique many times longer than broad, strongly compressed, valves 1-nerved, dehiscent at base only; seeds several to many per locule, uniseriate.

A monotypic genus of western North America.

Streptanthella longirostris (S. Wats.) Rydb. [*Arabis longirostris* S. Wats.; *Streptanthus longirostris* (S. Wats.) S. Wats.; *Euklisia longirostris* (S. Wats.) Rydb.; *Thelypodium longirostris* (S. Wats.) Jepson] Annual, stems erect or ascending, usually branched throughout, 1-5 dm tall; leaves 1.5-8.5 cm long, 0.1-1.2 cm wide, oblanceolate to elliptic or lance-linear, sinuate-dentate to entire, lower ones usually deciduous by anthesis, reduced upwardly; pedicels 1.5-6 mm long, curved in fruit; sepals 2-4.8 mm long, greenish or purplish, with scarious margins; petals 5-8 mm long, white with purplish veins; siliques 30-60 mm long, 1.5-2 mm wide, reflexed-descending, valves narrowed apically into an indehiscent beak 3-7 mm long; style obsolete. —Sandy, clayey, or gravelly soils in desert shrub, pinyon-juniper, and low elevation grassland communities from 900 to 1900 m elevation in Beaver, Carbon, Emery, Garfield, Grand, Kane, Millard, San Juan, Sevier, Uintah, Washington, and Wayne counties; Washington east to Wyoming and southward to Baja California and New Mexico.

STREPTANTHUS Nutt.

Plants glabrous, perennial, arising from taproots, rarely rhizomatous; leaves alternate and basal, simple, dentate to entire, basal ones petiolate, upper ones becoming sessile, entire, and auriculate upwardly; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, chestnut to brown-purple or purple; stamens 6, often in 3 pairs as regards length and position, filaments lacking glandular processes; styles conspicuous, expanded, stigma bilobed; fruit a short-stipitate silique many times longer than broad, much flattened, valves with one main nerve and more or less reticulate lateral nerves; seeds several to many per locule, uniseriate.

A genus of perhaps 25 species of the western United States.

Streptanthus cordatus Nutt. ex Torr. & Gray. [*Euklisia cordata* (Nutt.) Rydb.; *Cartiera cordata* (Nutt.) Greene; S. *crassifolia* Greene] Perennial, stems not inflated, 1.8-5.7 (8) dm tall, glabrous and glaucous; basal leaves 1.5-8 (15) cm long, 0.5-2 (5) cm wide, spatulate to obovoid or oblanceolate, variously dentate, often sharply ciliate at least basally; cauline leaves becoming sessile and auriculate, ovate to oval or lanceolate; pedicels 4-9 mm long, ascending, glabrous; sepals (5) 7-10.5 mm long, usually purplish, glabrous except apically; petals 10-14.5 mm long, purple to chestnut, broad claw not constricted at juncture of blade, ascending to recurved; siliques 50-85 mm long, 3-5.8 mm wide, ascending to erect, glabrous; styles 1-3 mm long, expanded upwards, the stigma bilobed. —Sagebrush and pinyon-juniper communities from 1200 to 2600 m elevation in most of the counties of Utah; Oregon to Wyoming south to California, Arizona, and New Mexico.

A specimen collected near Kanosh, Millard County, by Pickford (*130*-OGDF) is definitely rhizomatous.

THELYPODIOPSIS Rydb.

Plants glabrous or pubescent with simple hairs, annual or biennial to perennial, arising from taproots; leaves alternate or alternate and basal, simple, oblong-oblanceolate to lanceolate or ovate, toothed to entire, petiolate or sessile and auriculate or merely sessile; flowers in racemes, pedicels ascending or spreading-ascending, not subtended by bracts except in some lowermost flowers; sepals 4, deciduous; petals 4, white, pink, lavender, or yellow; stamens 6, filaments lacking processes; style expanded upwards, stigma bilobed; fruit a sessile to stipitate silique, many times longer than broad, subterete to terete, valves 1 (3-5)-nerved; seeds uniseriate.

A genus of western United States and perhaps northern Mexico of perhaps seven species.

The species included herein have been treated as members of *Streptanthus*, *Thelypodium*, an expanded *Sisymbrium*, and even *Caulanthus*. The generic problem has been reviewed by Al-Shebaz (1973; see *Thelypodium*), but the solution adopted by that author, and followed in part here, is not altogether acceptable for our species. We have placed the wholly discordant *Caulanthus divaricatus* Rollins in *Thelypodiopsis*, and as *Thelypodium sagittatum* mirrors both *Thelypodiopsis elegans* and *T. ambigua* that entity might well be placed in the latter genus also.

1. Leaves merely sessile, not auriculate, all cauline; plants perennial, from a branching caudex .... *T. argillacea*
   Leaves auriculate, at least the cauline; plants biennial or winter annual 2

2(1). Petals yellow 3
   Petals pink, lavender, or white 4

3(2). Pedicels, sepals, and siliques glabrous; petal blade not especially constricted at juncture with petaloid claw .... *T. aurea*
   Pedicels, sepals, and siliques sparingly villous; petal blade conspicuously constricted at juncture with broadened membranous claw .... *T. divaricata*

4(2). Pedicels, sepals, and siliques glabrous; basal leaves often over 6 times longer than broad; plants known from Kane County .... *T. ambigua*
   Pedicels, sepals, and siliques sparingly villous; basal leaves usually less than 5 times longer than broad; plants of eastern Utah .... *T. elegans*

Thelypodiopsis ambigua (S. Wats.) Al-Shebaz. (*Thelypodium ambiguum* S. Wats.). Biennial or short-lived perennial, stems not inflated, 2-10 (12.5) dm tall, glabrous throughout; leaves basal and cauline, basal ones 3-15 (20) cm long, 0.6-2.8 cm wide, sinuate-dentate to entire, cauline ones reduced upwards, becoming entire and lance-ovate to lanceolate, 0.5-5.5 cm long, 0.3-1.8 cm wide, sessile and auriculate; pedicels 4-12 cm long, curved-ascending to spreading-ascending, glabrous; sepals 5-7 mm long, often pinkish-hyaline, glabrous, erect; petals 9-12 mm long, blade 3-4 mm wide, pink to lavender or white, claw broad, slightly constricted at juncture of blade; anthers 2.5-3.5 mm long; siliques 55-75 mm long, 1.2-2 mm wide, short-stipitate, terete, ascending to erect; styles 1-2.5 mm long, expanded upwards, stigmatic lobes developed. —Clay to sandy and gravelly soils in pinyon-juniper community from 1530 to 1830 m elevation in Kane (Eastwood & Howell 9300—US; Welsh & Atwood 9706—BRY) and Washington (Palmer 27, southern Utah, 1877—US) counties; Mohave County, Arizona.

Thelypodiopsis argillacea Welsh & Atwood. Plants perennial, glabrous, glaucous; stems 1.3-3 dm tall, simple or branched above, arising from a subligneous caudex; leaves sessile, all cauline, not auriculate, linear, 0.9-3 cm long, 0.8-2 mm wide, somewhat fleshy, entire, acute to rounded; racemes (5) 8- to 22-flowered; pedicels 7-13 mm long, ascending; sepals 4.2-6.5 mm long, purplish, margins hyaline; petals 7.8-10.9 mm long, 2.5-3.2 mm wide, white to lilac, with conspicuous purplish veins, claw not differentiated from the blade; anthers 1.7-2.5 mm long; siliques 18-25 mm long, 1-1.2 mm wide, subsessile, terete, ascending to erect; styles 0.5-1 mm long, expanded upwards, stigmatic lobes developed. Desert shrublands on Green River Shale, at lower elevations in Uintah County; endemic.

Thelypodiopsis aurea (Eastw.) Rydb. [*Thelypodium aureum* Eastw.; *Sisymbrium aureum* (Eastw.) Payson] Biennial or rarely short-lived perennial, stems not inflated, 1-7 dm tall, glabrous throughout or somewhat pubescent below with flattened, flexuous hairs; leaves basal and cauline, basal ones 2.5-6.5 cm long, 0.5-1.3 cm wide, irregularly toothed to subentire, cauline ones reduced upwardly, becoming entire and lanceolate to ovate-lanceolate, 1.3-6.5 cm long, 0.4-2.3 cm wide, sessile and auriculate; pedicels 5-9 mm long, spreading-ascending, glabrous; sepals 5-9.3 mm long, yellowish, glabrous, ascending; petals 6.9-12.5 mm long, blade not expanded, 1.5-3.5 mm wide, yellowish, claw very broad, ascending limb not especially constricted at juncture with claw; anthers 2.7-3.7 mm long; siliques 40-70 mm long, 1-1.5 mm wide, stipitate, stipe 2-7 mm long, terete, ascending to erect, glabrous; styles 1-3 mm long, expanded upwards, stigmatic lobes well developed. — Clay to sandy soils in semidesert shrub and pinyon-juniper communities from 1500 to 2450 m elevation in San Juan County; Colorado.

Thelypodiopsis divaricata (Rollins) Welsh & Reveal, comb. nov., based on *Caulanthus divaricatus* Rollins, Contr. Gray Herb. 201: 8. 1971. Biennial or winter annual, erect, simple, stems not inflated, 2-11 dm tall, herbage more or less pubescent with long, tangled hairs at least below; leaves basal and cauline, basal ones 1.5-10 cm long, 0.4-2.8 cm wide, irregularly toothed or rarely pinnatifid, subentire or dentate at apex only, cauline ones reduced upwardly, becoming entire and ovate-lanceolate, 0.7-9 cm long, 0.4-2.8 cm wide, sessile and auriculate; pedicels 5-21 mm long, spreading-ascending, sparingly villous to glabrate; sepals (3.5) 4.8-7 mm long, yellowish, sparingly villous; petals 7-10 mm long, yellowish, claw very broad, ascending limb constricted at juncture with claw; anthers 2.5-3.8 mm long; siliques 40-80 (90) mm long, 1-1.5 mm wide, sessile or subsessile, terete, ascending to erect, sparingly villous when young, becoming glabrous with age; styles 1-2 mm long, with stigma reduced or expanded and lobes not or only moderately well developed. — Clay soils in shadscale, blackbrush, and pinyon-juniper communities from 1280 to 1700 m elevation in Carbon, Emery, Garfield, Grand, San Juan, and Wayne counties; endemic.

Thelypodiopsis elegans (M. E. Jones) Rydb. [*Thelypodium elegans* M. E. Jones; *Sisymbrium elegans* (M. E. Jones) Payson; *Streptanthus wyomingensis* A. Nels.; *Thelypodiopsis wyomingensis* (A. Nels.) Rydb.] Biennial or rarely a winter annual or a short-lived perennial, stems 1.2-9.5 dm tall, almost or quite glabrous to densely pubescent below with flattened, flexuous hairs; leaves basal and cauline, basal ones 1-6.5 cm long, 0.3-1.5 cm wide, sinuate-dentate to irregularly toothed or entire, cauline ones reduced upwardly, becoming entire and lanceolate to ovate-lanceolate or oblong, 0.3-8.5 (12) cm long, 0.3-2 cm wide, sessile and auriculate; pedicels 5-18 mm long, curved-ascending to spreading-ascending, glabrous or sparingly villous, erect; petals 11-14.5 mm long, blade 3-6 mm wide, pink to lavender or white with pinkish veins, claw very broad, not constricted at juncture with blade; anthers 2.6-3.2 mm long; siliques 45-75 mm long, 1.2-1.8 mm wide, sessile or subsessile, terete, ascending to erect, glabrous or sparingly villous; styles 1.8-3 mm long, expanded upwards, stigmatic lobes well developed. —Clay, sandy, or gravelly soils in pinyon-juniper, sagebrush, and desert shrub communities from 1500 to 2300 m elevation in Duchesne, Grand, and Uintah counties; Wyoming, Colorado.

It has not been possible to segregate *T. wyomingensis* from the bulk of *T. elegans*, and that species is hereby reduced to synonymy.

THELYPODIUM Endl.

Plants glabrous or pubescent with simple hairs, annuals, biennials, or short-lived perennials, arising from taproots; leaves alternate and basal, simple, lyrate-pinnatifid, toothed or entire, petiolate or sessile, auriculate in some; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white, pink, lavender, or purple; stamens 6, filaments lacking glandular processes; styles slender to stout, cylindric to somewhat expanded upwards, stigmas small, entire or somewhat bilobed; fruit a stipitate silique many times longer than broad, terete or somewhat flattened, valves 1 (3)-nerved; seeds uniseriate.

A genus of about 10 species of western North America.

Pennellia micrantha (A. Gray) Nieuwl. [*Thelypodium micranthum* (A. Gray) S. Wats.; *Heterothrix micrantha* (A. Gray) Rydb.] has been repeatedly reported from Utah, but we have failed to find any specimens definitely known from the state in any of the herbaria we have consulted. It differs from the species of *Thelypodium* reported here in having stellately pubescent leaves.

Al-Shebaz, I. A. 1973. The biosystematics of the genus *Thelypodium* (Cruciferae). Contr. Gray Herb. 204 :3-148.

Payson, E. B. 1922. A monographic study of *Thelypodium* and its immediate allies. Ann. Missouri Bot. Gard. 9: 233-324.

1. Cauline leaves definitely auriculate 2
   Cauline leaves petiolate or sessile but not auriculate 3

2(1). Cauline leaves linear to oblong or oblong-lanceolate, appressed to stem; basal leaves 1-7 cm long, 0.4-1.8 cm wide .... *T. rollinsii*
Cauline leaves oblong to lanceolate, not appressed to stem; basal leaves 6-20 cm long, 0.6-5 cm wide .... *T. sagittatum*

3(1). Plants robust biennials, mostly 5-15 dm tall or more; racemes borne in corymbose panicles .... *T. integrifolium*
Plants various, but if (as rarely) as above, then racemes seldom if ever borne in corymbose panicles 4

4(3). Racemes mostly 1-8 dm long or more; petals 8 mm long or more, differentiated into a blade and claw; plants known only from Box Elder County .... *T. millefolium*
Racemes mostly less than 1 dm long; petals 4-8 mm long, hardly differentiated into a blade and claw; plants not of Box Elder County 5

5(4). Sepals ascending to spreading; petals 1.5-3.5 mm wide; eastern Utah .... *T. laxiflorum*
Sepals spreading to reflexed; petals 1-2 mm wide; Henry Mountains, Garfield County .... *T. wrightii*

Thelypodium integrifolium (Nutt.) Endl. Biennial, stems mostly 5-30 dm tall, simple or branched, glabrous and glaucous; basal leaves 5-30 cm long, 1.5-10 cm wide or more, spatulate to lanceolate, ovate or obovate, entire to denticulate; cauline leaves 2-12 (15) cm long, 0.2-2 cm wide, oblanceolate to elliptic or lanceolate, sessile, not auriculate; pedicels 3-10 mm long, variously spreading, strongly to moderately flattened at base; sepals 3-7 mm long, often purplish, glabrous; petals 5-10 mm long, mostly 1-2 mm wide, white to lavender or purple; anthers 1-3 mm long; siliques 10-45 mm long, 1-2 mm wide, stipitate, stipes up to 2 mm long; styles slender, 0.5-3 mm long; stigma entire. —Widespread at the lower elevations in Utah; common throughout much of the American West.

Four more or less distinctive varieties are known.

1. Mature fruiting pedicels whitish, stout; flowers white; plants of southwestern Utah .... *T. integrifolium* var. *affine*
Mature fruiting pedicels not whitish or only seldom so, slender or stout; flowers pink to lavender or white; plants not of southwestern Utah 2

2(1). Mature fruiting pedicels not or only somewhat flattened at base; plants mostly of south-central to north-central Utah .... *T. integrifolium* var. *integrifolium*
Mature fruiting pedicels strongly flattened at base; plants of eastern and southeastern or northwestern Utah 3

3(2). Racemes mostly 1-8 cm long in fruit; stipes often less than 1 mm long; plants of northwestern Utah .... *T. integrifolium* var. *complanatum*
Racemes mostly more than 8 cm long in fruit; stipes often more than 1 mm long; plants of eastern and southeastern Utah .... *T. integrifolium* var. *gracilipes*

Var. *affine* (Greene) Welsh & Reveal, comb. nov., based on *Thelypodium affine* Greene, Pittonia 4:314. 1901. [*T. rhomboideum* Greene; *Pleurophragma rhomboideum* (Greene) O. E. Schulz; *T. integrifolium* ssp. *affine* (Greene) Al-Shebaz]. Saline seeps, springs, irrigation canals, and stream sides from 850 to 1100 m elevation in Kane, Millard, and Washington counties; Nevada, California.

Var. *complanatum* (Al-Shebaz) Welsh & Reveal. [*T. integrifolium* ssp. *complanatum*

Al-Shebaz]. Uncommon, at lower elevations in Beaver and Box Elder counties; Utah westward to California and Oregon.

Var. *gracilipes* B. L. Robinson. [*T. gracilipes* (B. L. Robinson) Rydb.; *Pleurophragma gracilipes* (B. L. Robinson) Rydb.; *P. platypodium* Rydb., the type is from Moab; *T. rhomboideum* var. *gracilipes* (B. L. Robinson) Payson; *T. integrifolium* ssp. *gracilipes* (B. L. Robinson) Al-Shebaz]. Canyon bottoms, terraces, and hanging gardens at low elevations in Garfield, Grand, Kane, San Juan, Uintah, and Wayne counties; Arizona, Colorado, and New Mexico.

Var. *integrifolium*. [*Pachypodium integrifolium* Nutt. ex Torr. & Gray; *T. lilacinum* Greene; *Pleurophragma integrifolium* (Nutt.) Rydb.; *Pleurophragma lilacinum* (Greene) Rydb.; *T. lilacinum* var. *subumbellatum* Payson]. Marshes, seeps, stream sides, and other moist sites in Cache, Iron, Piute, Salt Lake, Sevier, and Utah counties; Washington east to the Dakotas and south to Oregon, Utah, Colorado, and Nebraska.

Thelypodium laxiflorum Al-Shebaz [*T. wrightii* var. *tenellum* M. E. Jones; *Stanleyella wrightii* var. *tenella* (M. E. Jones) Payson] Biennial, stems 1.5-15 dm tall or more, simple, glabrous throughout or hispid near base; basal leaves 3-15 cm long, 1-6 cm wide, pinnatifid to toothed; cauline leaves 3-9 cm long, 0.2-2 cm wide, subentire to entire, not auriculate; pedicels 4-13 mm long, spreading to descending, somewhat flattened at base; sepals 2.5-6 mm long, white to lavender, glabrous ascending to spreading; petals 4-8 mm long, 1.5-3.5 mm wide, white to lavender; anthers 1-3 mm long; siliques 20-75 mm long, 0.8-1.2 mm wide, stipitate, stipes 0.2-2 mm long; styles 0.5-2 mm long. —Mountain brush and forest communities from 1700 to 2450 m elevation in Carbon, Duchesne, Iron, Kane, San Juan, Utah (type from Slate Canyon), and Washington counties; Nevada to Colorado.

Closely related to *T. wrightii*.

Thelypodium milleflorum A. Nels. [*T. laciniatum* var. *milleflorum* (A. Nels.) Payson] Biennial, stems mostly 4-12 dm tall, almost always hollow, simple or branched, glabrous and glaucous; basal leaves 6-15 cm long, 1-7 cm wide, oblong to lanceolate or ovate, toothed or pinnatifid; cauline leaves similar to the basal ones only gradually reduced upwardly, petiolate, not auriculate; pedicels 2-6 mm long, curved-ascending, slightly flattened at base; sepals 4-9 mm long, creamy-white, glabrous; petals 8-15 mm long, 1-2 mm wide, white; anthers 2.5-5 mm long; siliques 25-85 mm long, 0.8-1.8 mm wide, stipitate, stipes 0.5-5 mm long; styles stout, 0.5-2 mm long; stigma entire. —Dry slopes and saline flats in Box Elder County; British Columbia south to California and east to Idaho and Utah.

Thelypodium rollinsii Al-Shebaz. Biennial, the stems (4) 5-16 (20) dm tall, simple or branched, glabrous and glaucous; basal leaves 1.3-7 cm long, 0.4-1.8 cm wide, spatulate to oblanceolate, toothed to subentire; cauline leaves 1-6 cm long, 0.1-0.8 cm wide, linear to narrowly lanceolate or oblong, erect, not flattened; sepals 4-7 mm long, lavender to purplish, glabrous; petals 6-10 mm long, 1.2-3 mm wide, lavender to purplish; anthers 2-4 mm long; siliques 20-60 mm long, 0.7-1 mm wide, stipitate, stipe 0.5-6 mm long; styles 0.5-2 mm long; stigma entire. —Stream terraces, saline flats, and seeps in greasewood and saltgrass communities from 1370 to 1700 m elevation in Carbon, Juab, Millard, Piute, Sanpete, and Sevier counties; endemic.

Thelypodium sagittatum (Nutt.) Endl. in Walpers. Biennial or short-lived perennial, stems 2-10 dm tall, rarely more, simple or more usually branched, glabrous or hirsute with simple hairs below; basal leaves 2-25 cm long, 1-5 cm wide, ovate to oblanceolate or oblong, entire; cauline leaves 0.7-10 (14) cm long, 0.2-2.8 cm wide, ovate to lanceolate or lance-oblong, entire, glabrous or puberulent especially on the veins, auriculate; pedicels 2.5-15 (20) mm long, spreading to spreading-ascending; sepals 2.5-10 mm long, green to purplish, glabrous; petals 5-15 mm long, 1-4 mm wide, white to lavender or purple; anthers 1.5-5 mm long; siliques 10-65 mm long, 0.5-1.2 mm wide, stipitate, stipes 0.3-2 mm long; styles 0.5-3 mm long. —Widespread in the state; Washington south to California and eastward to Montana and Wyoming.

This species simulates *Thelypodiopsis elegans* in some features and care should be taken in distinguishing the two. The species is divisible into three more or less distinctive varieties in Utah.

1. Petals linear to oblanceolate, 1.5 mm wide or less; pedicels 2.5-9 mm long; plants of southwestern Utah ....*T. sagittatum* var. *ovalifolium*

Petals oblanceolate to spatulate, 1-4 mm wide; pedicels 5-15 mm long or more; distribution various 2

2(1). Petals pink to lavender or purplish, or white fading lavender to purplish or white; siliques straight to curved, not or only slightly torulose .... *T. sagittatum* var. *sagittatum*

Petals white to pink, fading yellowish on drying; siliques flexuous-contorted and definitely torulose, wormlike .... *T. sagittatum* var. *vermicularis*

Var. *ovalifolium* (Rydb.) Welsh & Reveal. [*T. ovalifolium* Rydb., type from Panguitch Lake; *T. palmeri* Rydb., type from southern Utah; *T. sagittatum* ssp. *ovalifolium* (Rydb.) Al-Shebaz]. Clay soils in Garfield, Iron, and Kane counties; Nevada.

Var. *sagittatum.* [*Streptanthus sagittatus* Nutt.; *Pachypodium sagittatum* (Nutt.) Nutt. ex Torr. & Gray; *T. nuttallii* S. Wats.; *T. amplifolium* Greene; *T. torulosum* Heller; *T. macropetalum* Rydb., type from Davis County; *Thelypodiopsis nuttallii* (S. Wats.) O. E. Schulz; *Thelypodiopsis torulosa* (Heller) O. E. Schulz]. Clay or silty, often saline, soils from 1200 to 2300 m elevation in Box Elder, Cache, Davis, Duchesne, Salt Lake, Summit, Tooele, Utah, and Wayne counties; Washington and Montana south to Nevada, Utah, and Colorado.

Var. ***vermicularis*** Welsh & Reveal, var. nov. A *Thelypodio sagittato* var. *sagittato* petalis discoloriter flavidis et siliquis flexuosis et torulosis differt. Holotype: Utah: Sevier County, about 4 miles southeast of Sigurd along Utah Highway 24, on the Arapien Shale Formation in a greasewood community, 29 May 1972, Welsh & Atwood 11718. Holotypus, BRY. Paratypes: Utah: Box Elder County, Grouse Creek, 27 May 1973, *Albee 1355;* Juab County Fish Springs Range, 9 May 1968, Reveal & Thomas 984 (BRY, US); Millard County, west of Hinckley, 19 Apr 1930, *Cottam 4622;* 2 miles south of Black Rock Station, 14 May 1968, *R. C. Holmgren 534;* Sevier County, Glenwood, 18 May 1875, *Ward s.n.* (US); Utah County, Coyote Pass, 1.2 mile west of Utah Highway 68, 15 May 1968, *Weston 71* (all BRY unless otherwise indicated); endemic to Utah.

Thelypodium wrightii A. Gray. [*Stanleyella wrightii* (A. Gray) Rydb.] Biennial, stems 1.5-10 dm tall or more, simple or more commonly branched, glabrous throughout or hispid near the base; basal leaves 3-15 cm long, 1-6 cm wide, pinnatifid to lyrate-pinnatifid; cauline leaves 3-9 cm long, 0.2-2 cm wide, pinnatifid to sinuate-dentate, rarely subentire, not auriculate; pedicels 4-13 mm long, spreading to descending, somewhat flattened at base; sepals 2.5-6 mm long, white to lavender, glabrous, spreading to reflexed; petals 4-8 mm long, 1-2 mm wide, white to lavender; anthers 1-3 mm long; siliques 20-75 mm long, 1-1.5 mm wide, stipitate, stipes 0.2-2 mm long; styles 0.5-1 mm long. —Rare and isolated in Utah well away from the bulk of range of this species, known only from a M. E. Jones collection from the Henry Mountains, Garfield County; Colorado and Arizona eastward to Texas and northern Mexico.

THLASPI L.

Plants glabrous, annual or perennial, arising from taproots; leaves cauline or cauline and basal, alternate, simple, entire to dentate or lobed; flowers racemose, pedicels not subtended by bracts; sepals 4, deciduous; petals 4, white, sometimes pinkish or lavender; stamens 6, filaments lacking glandular processes; fruit a sessile silicle, compressed contrary to septum, often more or less wing-margined; style obsolete or slender and conspicuous, stigma capitate; seeds 2 to several per locule, uniseriate.

A genus of perhaps 50 species, mostly of Eurasia.

Holmgren, P. K. 1971. A biosystematic study of North American *Thlaspi montanum* and its allies. Mem. New York Bot. Gard. 21:1-106.

Payson, E. B. 1926. The genus *Thlaspi* in North America. Univ. Wyoming Publ. Bot. 1:145-186.

1. Plants annual; styles obsolete or up to 0.2 mm long; fruit orbicular in outline, conspicuously winged .... *T. arvense*
   Plants perennial; styles 0.3-2.5 mm long or more; fruit oblanceolate to obcordate or obovate in outline, narrowly wing-margined or not winged at all .... *T. montanum*

Thlaspi arvense L. Annual, stems mostly 1-7 dm tall; basal leaves usually deciduous by anthesis; cauline leaves 1-8 cm long, 0.2-2.5 cm wide, elliptic to lanceolate or oblanceolate, sinuate-dentate to pinnatifid or subentire, uppermost sessile and auriculate; pedicels 5-12 mm long or more, spreading to curved-ascending; sepals 1.5-2.5 mm long, green with whitish margins; petals 3-4.5 mm long, white; silicles 10-17 mm long, 7-12 mm wide, strongly compressed, wing-margined all around; styles almost obsolete. —Weedy species of roadsides, meadows, fields, and other disturbed places from 1370 to 2450 m elevation in Box Elder, Cache, Davis, Grand, Rich, Salt Lake, Utah, Wasatch, and Weber counties, and to be expected elsewhere; widespread in North America; adventive from Europe.

Thlaspi montanum L. [*T. alpestre* of authors, not L.; *T. cochleariforme* DC.; *T. nuttallii* Rydb.; *T. alpestre* var. *glaucum* A. Nels.; *T. glaucum* (A. Nels.) A. Nels.; *T. coloradoense* Rydb.; *T. purpurascens* Rydb.; *T. alpestre* var. *purpurascens* (Rydb.) Ostenf.; *T. glaucum* var. *pedunculatum* Payson; *T. glaucum* var. *hesperium* Payson; *T. hesperium* (Payson) G. N. Jones; *T. fendleri* var. *coloradoense* (Rydb.) Maguire; *T. fendleri* var. *tenuipes* Maguire, type from Sanpete County; *T. fendleri* var. *hesperium* (Payson) C. L. Hitchc.] Perennial, with simple or branched caudex branches, stems 0.2-4 dm tall; basal leaves 0.9-3.5 cm long or more, 0.2-1 (1.5) cm wide, oval to oblong or spatulate-oblanceolate; cauline leaves 0.5-2.5 cm long, 0.1-1.2 cm wide, sessile and auriculate; pedicels 2-15 mm long, spreading or spreading-ascending; sepals 1.5-3.5 mm long, greenish to purplish; petals 3.5-7.5 mm long, white, pinkish or lavender, spatulate; silicles 3-8 mm long, rarely more, 1.5-5 mm wide, obovate to obcordate, winged or not so; styles 0.5-2.5 mm long. —Forest, krumholz, and alpine tundra communities from 2150 to 3965 m elevation in Beaver, Box Elder, Davis, Daggett, Duchesne, Emery, Garfield, Grand, Iron, Kane, Piute, Salt Lake, San Juan, Sanpete, Sevier, Summit, Tooele, Uintah, Utah, Wasatch, Washington, and Weber counties; Washington east to Montana and south to California, Arizona, New Mexico, and Texas; Eurasia.

Our material belongs to var. *montanum*. Some specimens from the southern part of the state approach the more southern var. *fendleri* (A. Gray) P. K. Holmgren, which has styles longer than 2.5 mm in length, petals 6-13 mm long, and silicles 7-16 mm long and 4-9 mm wide.

THYSANOCARPUS Hook.

Plants glabrous or pubescent with simple hairs, annual, arising from taproots; leaves cauline, alternate, simple, oblong-lanceolate to linear, toothed to entire; flowers racemose, pedicels recurved and not subtended by bracts; sepals 4, deciduous; petals 4, white or tinged pink or purple; stamens 6, the filaments lacking glandular processes; fruit a strongly compressed, unilocular, 1-seeded, indehiscent silicle, margin winged.

About 5 species of western North America.

Thysanocarpus curvipes Hook. Annual, stems 1-5 dm tall or more, simple or branched, sometimes hirsute below, otherwise glabrous; leaves 1.2-5 cm long, 0.1-1 cm wide, lance-oblong to elliptic or linear, sinuate-dentate to entire, transitional upwards to smaller sessile and auriculate blades; pedicels 3-7 mm long, recurved in fruit; sepals 1-1.5 mm long, often purplish; petals 1.5-2 mm long, white or tinged purplish or pinkish; silicles 4.5-8 mm long, 3-4 mm wide, ovate to obovate, often plano-convex, glabrous or pubescent, wing crenate and sometimes perforate; styles 0.4-0.6 mm long. —Sand and gravelly soils in the warm desert shrub communities from 670 to 975 m elevation in Washington County; British Columbia south to California and eastward to Utah and Arizona.

Our material belongs to var. *eradiatus* Jepson.

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TYPHLODROMUS MCGREGORI CHANT (ACARINA: PHYTOSEIIDAE) AND ITS CONTROL OF PHYTOPHAGOUS MITES IN UTAH AND SOUTHERN CALIFORNIA APPLE ORCHARDS[1]

B. A. Croft[2] and C. D. Jorgensen[3]

Abstract.—A review of published and unpublished data for the predatory mite *Typhlodromus mcgregori* in Utah and southern California apple growing areas is presented to summarize its role. *Typhlodromus mcgregori* was not found resistant to pesticides and, although usually present with *Bryobia rubrioculus*, only when *Aculus schlechtendali* was also present was there significant predation on *B. rubrioculus*. *Aculus schlechtendali* was considered the primary host and *B. rubrioculus* secondary for *T. mcgregori*. *Typhlodromus occidentalis* was always found associated with *Tetranychus* spp. and often with *Eotetranychus* and *Pronematus ubiquitus* in unsprayed orchards.

Certain phytoseiid mites are specialized predators of phytophagous mites and are capable of controlling or suppressing their populations at low densities (Collyer 1964, Hoyt 1969, Croft and Barnes 1971). This potential for biological control has prompted studies of the native species in many agricultural areas of the world (Huffaker et al. 1969), and, although predator-prey relationships vary in different geographic regions, similar associations are not uncommon in areas where ecological conditions are similar.

During 1967-70, Jorgensen and co-workers (Jorgensen 1968, Nelson and Jorgensen 1968, Croft and Jorgensen 1969, Leetham and Jorgensen 1971, and Duke et al. 1970) investigated predator-phytophagous mite relationships in Utah apple orchards. They reported *Typhlodromus mcgregori* Chant and *T. occidentalis* Nesbitt in predatory association with *Bryobia rubrioculus* Scheuten and *Tetranychus mcdanieli* McGregor, respectively.

Croft (1970) found predator-prey relationships in mountain apple orchards of southern California (Oak Glen, near Yucaipa, Calif.) almost identical to those reported in Utah. Because of this and similar native vegetation, he concluded that the Oak Glen environment was an extension of the ecological type reported for Utah, and atypical of other apple areas in California. His conclusions were also influenced by the common occurrence of *Tet. mcdanieli* throughout Utah and at Oak Glen. This species is not reported from other apple areas of California (Barnes and Madsen 1961). These similarities allow for the summary of both areas in this single analysis and should provide a general understanding of the role occupied by *T. mcgregori*.

Although different techniques were used, both Jorgensen's group and Croft studied the ecology, bionomics, and control effectiveness of *T. mcgregori*. This paper presents additional data and a summary of the predator-prey relationships, along with the apparent role of *T. mcgregori* in both areas. Although *T. occidentalis* was an effective natural enemy of *Tet. mcdanieli* in both regions, references to this predator are limited to comparisons of predator effectiveness or possible niche overlaps with *T. mcgregori* and their respective relationships to the total ecology of mites in the orchards studied.

General Methods

Investigations in southern California were conducted at Oak Glen, an apple growing area *ca* 12.9 km north of Yucaipa, California, at the eastern edge of the Los Angeles basin, and included about 162 ha of commercial apples grown between 1341-1463 m in the San Bernardino Mountains. Predominant apple varieties in both areas include Delicious, Rome Beauty, and Jonathan. Vegetation types in the southern California study area were typical of those in valleys of more northern latitudes in Utah, i.e., *Acer negundo*, *Prunus virginiana*, *Pinus ponderosa*, and *Symphorocarpus albus*.

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Studies on the effects of pesticide treatments on, and the biologies of, certain pest species had previously been conducted in the Oak Glen orchards (Barnes and Madsen 1961). During the summers of 1968-70, sampling studies emphasizing both pedator and prey mite relationships were made. Seven unsprayed, neglected orchards and 11 sprayed orchards, all of the Delicious variety, were sampled at two-week intervals from 13 June to 24 Oct 1968. Spur samples (50 spurs/tree) with leaves were processed using Berlese extraction methods and mites mounted for identification.

During the summers of 1969 and 1970 a series of orchards, including one which had not been sprayed for 10 years, three which had not been sprayed for 3-5 years, and one under a commercial chemical control program, were sampled at two-week intervals to determine population trends of both pest and predatory mites. In samples from five orchards, 20 leaves were collected from five locations of the four compass zones in each of five trees (80 leaves/tree) during the summer. All population counts were made by direct observation through a binocular microscope or from plates of the mite-brushing machine.

In addition to the field studies in California, evaluations of the oviposition rates and developmental times for *T. mcgregori* from egg to adult, when reared on several eriophyid rust mite species, were made in the laboratory. Oviposition rates/female predator for an eight-day period (replicated 10 times ea) when confined on excised apple, peach, or pear leaves containing populations of *Aculus schlechtendali* (Nalepa), *A. coronutus* (Banks), or *Eriophyes pyri* (Pgst.), respectively, at densities of ca 200 rust mites per leaf were determined. Developmental rates for *T. mcgregori*, using four replications with 10 females/replicated leaf when feeding only on *A. schlechtendali* at densities of 200/leaf, were also measured. In all experiments the temperatures were24 ± 2 C and the RH 30-60 percent.

In Utah, two types of studies were conducted. First, an extensive examination of mite distributions and species associations was made (Jorgensen 1968, Nelson and Jorgensen 1968, Leatham and Jorgensen 1971, Duke et al. 1970); however these were only correlative comparisons, and no experiments were done to measure specific associations between the various predator and prey mite populations. Attention was not given to the possibility that rust mites were preferred by *T. mcgregori*. Second, the life history of *T. mcgregori* was studied by Croft and Jorgensen (1969), using *B. rubrioculus*, *Tet. mcdanieli*, and *Panonychus ulmi* Koch as experimental food bases. Again, rust mites were not used as food in these experiments.

RESULTS AND DISCUSSION

Mite Fauna at Oak Glen

Mite species collected commonly from unsprayed Oak Glen apple orchards were: Tetranychidae—*Tet. mcdanieli*. *B. rubri*oculus, and *Eotetranychus uncatus* Garman; Phytoseiidae— *T. mcgregori*, *T. occidentalis*, and *T. pomi* (Parrott); and Tydeidae— *Pronematus ubiquitus* (McGregor); Eriophyidae— *A. schlechtendali*; and Erythraeidae— *Belaustium* sp. *Tetranychus mcdanieli* was collected predominantly from commercial orchards which were intensively sprayed with pesticides. Barnes and Madsen (1961) noted the absence of *P. ulmi* from Oak Glen, an observation that was supported during our work.

Unsprayed for Ten Years.— Population levels of phytophagous and predatory mites were extremely variable among trees in this orchard during 1969 and 1970, and for this reason separate plots for two different tree groupings are reported. In three trees during 1969 (Fig. 1A), *B. rubrioculus* attained high population levels of *ca* 40/leaf while only very low populations of *T. mcgregori* developed in late season. In 1970, mites in these same trees showed similar population trends for these two species; however, brown mites only increased to *ca* 15/leaf while *T. mcgregori* was more abundant and reached 0.8/leaf in August (Fig. 1B).

During 1969 (Fig. 1C) and 1970 (Fig. 1D), in two other trees in this orchard, populations of *A. schlechtendali* were present in addition to *B. rubrioculus* and *T. mcgregori.* In these instances, *B. rubrioculus* attained lower peak levels and *T. mcgregori* exhibited a more marked numerical response as compared with the situation when *A. schlechtendali* was not present (i.e., compare data of 1A and B with 1C and D). Although *Tet. mcdanieli* was occasionally found in unsprayed blocks, it was not collected in this orchard, nor was *T. occidentalis.*

Unsprayed from Three to Five Years.—Figures 2A and 2B show the mean densities of *Tet. mcdanieli-Eotetranychus uncatus* (collectively referred to as *Tet. mcdanieli* in Figures 2A and 2B because *E. uncatus* was only present at low densities) and *B. rubrioculus* populations in two apple orchards for the 1969 season. These species were separated temporally; *B. rubrioculus*, with an early season distribution, reached its peak density in July, whereas the *Tet. mcdanieli-E. uncatus* populations began to increase in July and peaked in late August or early

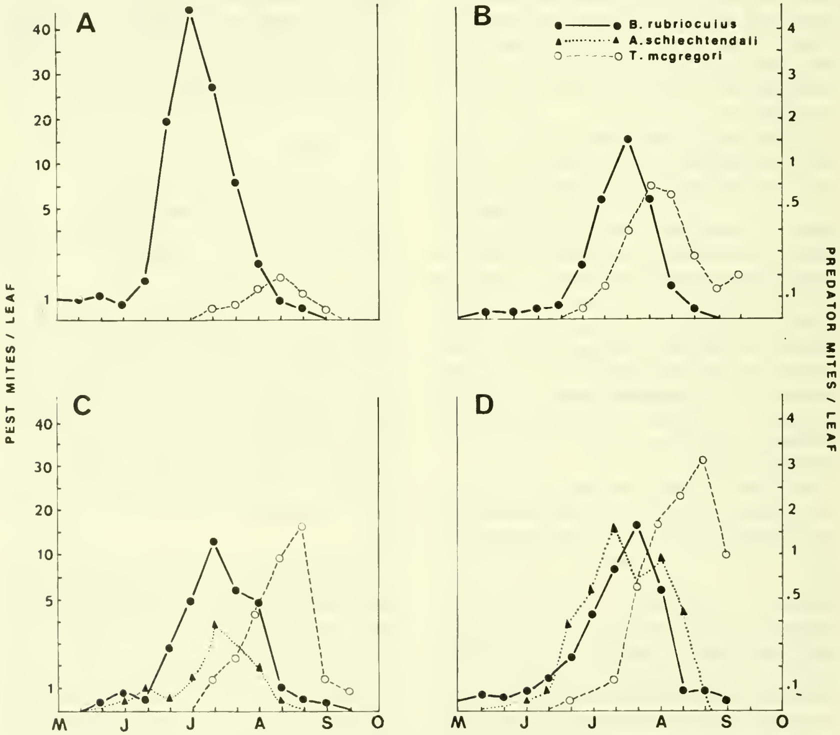

Fig. 1. Densities of plant-feeding and predaceous mites in an apple orchard unsprayed for 10 years at Oak Glen, California: pooled values for three trees during the 1969 (A) and 1970 seasons (B); pooled values for two other trees during the 1969 (C) and 1970 (D) season.

September. The apple rust mite, *A. schlechtendali*, was present in the trees, but almost at undetectable levels. Although both *T. mcgregori* and *T. occidentalis* occurred in these orchards, *T. mcgregori* did not respond markedly to increasing densities of any tetranychid species, whereas *T. occidentalis* populations appeared to increase with increases in the densities of *Tet. mcdanieli-E. uncatus* populations and eventually overcame their populations before they exceeded three to five mites per leaf.

In the other orchard unsprayed for three to five years, *B. rubrioculus* occurred only at very low densities (2 mites/leaf) and *T. mcgregori* was seldom found (Fig. 2C). Rust mites were only occasionally observed in this block (not plotted in Fig. 2C). In Figure 2C the tetranychid mites, *Tet. mcdanieli* and *E. uncatus* began increasing in late July and early August, with an apparent numerical response by *T. occidentalis*. Predator populations increased to nearly 3/leaf before declining to a lower density as prey became scarce. The tydeid, *P. ubiquitus*, increased to a density of 0.6/leaf during the period when the populations of tetranychids were greatest. The presence of both tetranychids and tydeids appeared to provide prey for the observed numerical increase in

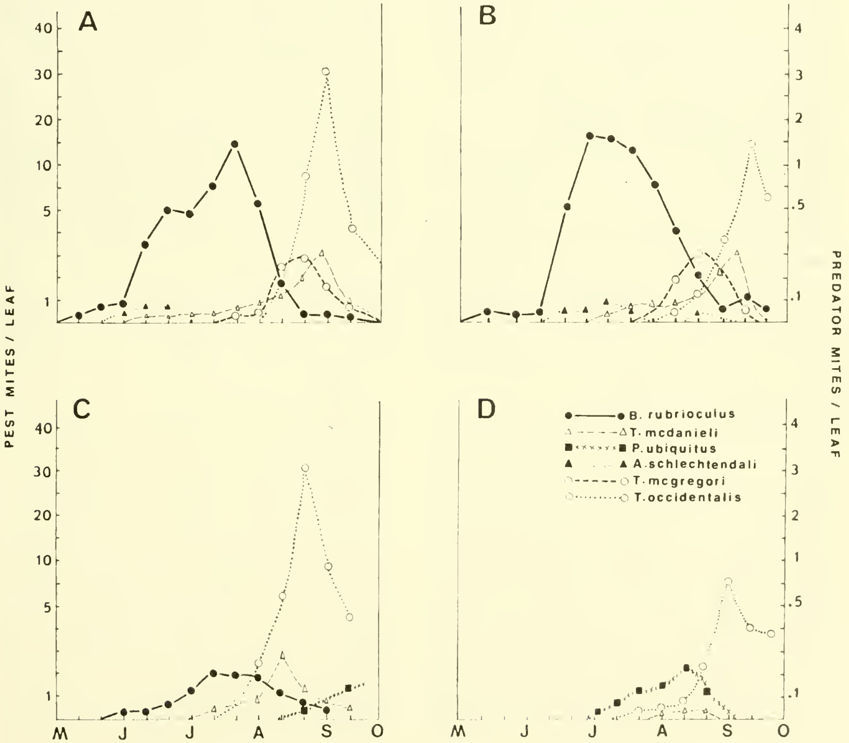

Fig. 2. Densities of plant-feeding and predaceous mites in four apple orchards unsprayed for 3-5 years at Oak Glen, California, during 1969 (A, B, and C) and 1970 (D): represents pooled values for 5 trees/orchard.

the predator populations, as *T. occidentalis* were frequently observed feeding on the tydeids.

In Figure 2D, *P. ubiquitus* populations attained 2.6/leaf and were the major prey supporting the populations of *T. occidentalis*, which increased to 0.8/leaf on 19 September. In this orchard, *Tet. mcdanieli-E. uncatus* populations did not exceed 0.3/leaf during the entire season and virtually no *B. rubrioculus* were observed.

Commercially Managed Orchards.— Figures 3A and 3B illustrate the population densities of *Tet. mcdanieli* throughout the summers of 1969 and 1970, in a sprayed orchard without any phytoseiid mites. *Tetranychus mcdanieli* exceeded 100/leaf in total orchard samples and, on occasion, exceeded 1,000 mites on individual leaves. If miticide sprays were not applied, intraspecific competition for food finally limited their increases, but only after severe damage to the apple foliage had been sustained.

During the summers of 1968 and 1969, over 200 samples (50 leaf spurs/sample) were taken from 19 other sprayed apple orchards. Less than 50 phytoseiid mites were collected from the foliage of apple trees at these sites, approximately equal numbers of *T. mcgregori* and *T. occidentalis*. Most of these predators were taken from peripheral trees which were near native, unsprayed vegetation. Predators were encountered only late in the growing season after pesticide residues were dissipated.

Although the selection of sites and the presentation of data in Figures 1-3 oversimplify the ecological differences between sprayed and unsprayed orchards at Oak Glen, California, the following species assessments were concluded from these data:

Bryobia rubrioculus was collected only in unsprayed orchards and was most abundant during the early summer. *Aculus schlechtendali* occurred at low levels in unsprayed plantings and varied greatly among locations from year to year. It was also observed at low densities in commercial orchards. Unsprayed orchards were never observed where *A. schlechtendali* occurred without *B. rubrioculus*, although some orchards supported *B. rubrioculus* only. *Tetranychus mcdanieli* was found most commonly in sprayed apple orchards in late summer when populations attained extremely high densities and caused serious damage to apple foliage in the absence of sufficient phytoseiid mites or adequate chemical control. This species and low densities of *E. uncatus* were also found in unsprayed trees where the tydeid mite, *P. ubiquitus*, was sometimes observed.

Typhlodromus mcgregori was always found in unsprayed orchards where *B. rubr-*

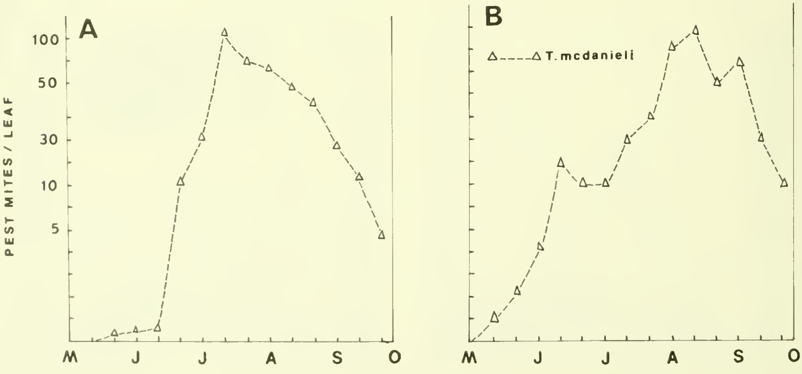

Fig. 3. Densities of *Tetranychus mcdanieli* in a sprayed commercial apple orchard at Oak Glen, California, during 1969 (A) and 1970 (B); represents pooled values for 5 trees.

ioculus occurred. The predators appeared to prey on this species, but they did not suppress its densities significantly. When *A. schlechtendali* was present with *B. rubrioculus*, *T. mcgregori* rapidly increased in response to the rust mites and seemed to suppress *B. rubrioculus* populations to a greater extent than when rust mites were absent. With the exception noted above, *T. occidentalis* was collected almost exclusively from unsprayed orchards where it was most closely associated with population complexes of *Tet. mcdanieli*, and *E. uncatus*, which were effectively maintained at low levels by the predator. *Pronematus ubiquitus* also appeared to be an adequate alternate host for *T. occidentalis* in several unsprayed orchards. Although Hoyt (1969) and Burrell and McCormick (1964) reported *A. schlechtendali* as a favorable prey species for *T. occidentalis*, the predator was never found in orchards at Oak Glen where only rust mites or *B. rubrioculus* were present. Only in one case in Utah was *T. occidentalis* found associated with *B. rubrioculus* and *A. schlechtendali*, and it was in a mixed block of apples, plums, and peaches along with high populations of rust mites and *Eotetranychus carpini borealis* Pritchard and Baker. We concluded from these data, as did Burrell and McCormick (1964), that *B. rubrioculus* probably is not an acceptable prey for *T. occidentalis*.

These observations and conclusions in relation to the bionomics of these species follow closely with those of Croft and Jorgensen (1969) and Duke et al. (1970), who reported the relationship of *T. mcgregori* in close association with *B. rubrioculus* in unsprayed apple orchards in Utah; and yet *T. mcgregori* did not exert any significant control of the prey. The association of *T. occidentalis* with *Tet. mcdanieli* and/or *E. uncatus* or closely related species was reported earlier by Hoyt (1969) for *T. occidentalis*-*Tet. mcdanieli*, Schuster and Pritchard (1963) for *T. occidentalis*-*Tet. pacificus* McGregor or *Eotetranychus willamettei* (McGregor), and Flaherty (1967) for *T. occidentalis*-*T. pacificus* or *E. williamettei*. In no instance, has *T. occidentalis* been reported as a predator of *B. rubrioculus*, yet this predator occurs in many geographical regions where *B. rubrioculus* is found.

One additional result which provides insight into the role of *T. mcgregori* as a predator of orchard pests relates to its relatively high oviposition rate/female/day when feeding on each of the three eriophyids: *A. schlechtendali* = 2.0 ± 0.2, *A. coronutus* = 1.9 ± 0.3, and *E. pyri* = 2.0 ± 0.1. The greatest average egg production observed for a 24-hour period was 2.3, which probably is close to the maximum for this species. Mean developmental time (egg-egg) for four replications of 10 *T. mcgregori*/replication feeding on *A. schlechtendali* were 8.5, 8.7, 8.0, and 8.5 days for an overall mean of 8.42 ± 0.3 hrs.

THE ROLE OF TYPHLODROMUS MCGREGORI: A REEVALUATION

Typhlodromus mcgregori occurs throughout North America north of Mexico and has been collected from several native plants in addition to walnut, grape, fig, apple, and citrus (Schuster and Pritchard 1963, Duke et al. 1970). Reported prey for this pedator includes *Aegyptobia nothus* P. and B., *Tet. pacificus*, *Eoteteranychus boudreauxi* P. and B., *Eriophyes vites* Pgst., *E. williamettei* and *B. rubrioculus* (Poe and Enns 1969, Schuster and Pritchard 1963, Duke et al. 1970).

Croft and Jorgensen (1969) studied the life history of *T. mcgregori* while it fed on *B. rubrioculus*, *P. ulmi* and *T. urticae* and observed that it preferred *B. rubrioculus* as compared to *P. ulmi* and *T. urticae*. They concluded that *T. mcgregori* did not assist substantially in controlling the latter two pests which occurred primarily in sprayed apple orchards in Utah. Even when feeding on *B. rubrioculus*, which *T. mcgregori* seemed most closely associated with in unsprayed orchards, the rate of development and oviposition rates were considerably lower than reported values for most other phytoseiid species which are efficient predators of tetranychid mites (McMurtry et al. 1970).

Duke et al. (1970) examined the distribution of *T. mcgregori*: (1) among apple orchards in Utah, (2) within apple orchards,

(3) within apple trees, and (4) upon apple leaves. They also reported the searching behavior of *T. mcgregori* on apple leaves. Predators were found principally in unsprayed orchards, aggregated within orchards, uniformly distributed within trees but nonuniformly upon leaves, and they searched leaves in a restrictive manner. In all cases, the predator distribution and searching behavior failed to closely correspond with movements and distributions of *B. rubrioculus*.

Nelson and Jorgensen (1968) further studied the dispersal and distributional associations between *T. mcgregori* and *B. rubrioculus* and found little or no correlation between predators and prey on spurs and leaves during the entire year or over a single 24-hour period. *Bryobia rubrioculus* was extremely mobile and present over a greater portion of the apple tree than was *T. mcgregori*.

To summarize, Jorgensen and co-workers listed three factors which contributed to the observed inability of *T. mcgregori* to appreciably affect or control populations of *B. rubrioculus* in the field: (1) *T. mcgregori* was limited in its reproductive and destructive ability when compared to the reproductive potential of *B. rubrioculus* (Croft and Jorgensen 1970); (2) *T. mcgregori* had limited potential for controlling *B. rubrioculus* because of differences in respective distributions in orchards, trees, and leaves and the predators' restricted searching behavior (Duke et al. 1970); and (3) *T. mcgregori* had dissimilar dispersal habits and spring distributions as compared to *B. rubrioculus*, which was more active and present over a greater portion of foliage and woody areas of apple trees (Nelson and Jorgensen 1968).

Considering the three factors suggested by Jorgensen and co-workers and in light of the data presented herein, we can now reevaluate the role of *T. mcgregori* as a predator of phytophagous mites in Utah and southern California apple orchards. We agree with Huffaker et al. (1969), who suggested that the comparative measure of oviposition between hosts and predators is only one aspect of a species rate of increase (*r*), and that *r* is only one component to the total predator response to its prey. Functional and numerical responses, and the subtractive effects of predation, must be considered in measuring the net effect of predation on a prey population. We do not consider the reduced oviposition rate of *T. mcgregori* when feeding on *B. rubrioculus* to represent a major limiting factor to its ability to control the latter, but rather its inefficiency is more likely explained by other means.

Both Duke et al. (1970) and Nelson and Jorgensen (1968) pointed out that the spatial occurrence (distribution and dispersal movement) of *T. mcgregori* was only loosely associated with that of *B. rubrioculus*. If the predator-prey association was primary, this incongruity would be an important factor in limiting effective predation. We now question the assumption of primary association altogether.

It is apparent that neither the Utah nor southern California strain of *T. mcgregori* are primarily adapted to the spider mites (e.g. *P. ulmi*, *Tet. urticae*, *Tet. mcdanieli*) which most commonly occur in sprayed orchards. Feeding studies by Croft and Jorgensen (1969) suggested a lack of association with *P. ulmi* or *Tet. urticae* for the Utah strain and population studies in both areas indicated little or no association with *Tet. mcdanieli*. Also, colonies of *T. mcgregori* do poorly in the laboratory when reared on *Tet. pacificus* (B. A. Croft, unpublished data).

The relationship between *T. mcgregori* and *B. rubrioculus* is unclear, since both species were consistently found together in unsprayed orchards during the growing season. It is not known whether this is a primary association and *B. rubrioculus* is the preferred prey, or a secondary association allowing for the maintenance of *T. mcgregori* populations at low levels, or an association which develops after predators respond to other species (e.g., *A. schlechtendali*). The latter question seems most likely considering the reproductive rates reported herein for *T. mcgregori* when feeding on three rust mite species, including *A. schlechtendali*. Croft and Jorgensen (1969) reported 11.5 days (egg-egg) for developmental time and 1.2 eggs/day/female for *T. mcgregori* when feeding on *B. rubrioculus.* When preying on *A. schlechtendali*, these predators developed about three days faster and oviposited *ca* 0.8 eggs/female more per day. Eriophyid mites also have been reported as equal to or more favorable prey than tetranychids for several other phytoseiid species (Chant 1959, Hoyt 1969, Burrell and McCormick 1964).

Huffaker et al. (1969) generalized that "some species of such mites (e.g. *Bryobia arborea*) seem highly immune to predators that are so efficient against certain species of *Panonychus* and *Tetranychus*. . . ." (*Bryobia arborea* Morgan and Anderson = *B. rubrioculus.*) Few workers have reported efficient predation between any phytoseiid species and *B. rubrioculus* (McMurtry et al. 1970), and reports of poor predation and reproduction are common (Herbert 1959, Burrell and McCormick 1964). Several features of the morphology, behavior, and biology of *B. rubrioculus* may account for this immunity, including the large size of the adult mites (McMurtry et al. 1970) and their highly mobile behavior, particularly the adults which spend a large portion of their time on the woody parts of the plant, where they lay many eggs (Nelson and Jorgensen 1968).

Typhlodromus mcgregori was seldom found on sprayed plantings in either study area, although *A. schlechtendali* occurred in both unsprayed and commercial orchards. Another contributing factor to its absence from sprayed orchards and its replacement in many areas other than Oak Glen by the predator, *T. occidentalis*, may be related to a differential susceptibility of these two predators to pesticides. *T. occidentalis* has developed resistance to many pesticides that are commonly applied for apple pest control in most fruit-growing areas where pesticides have been widely used (Croft and Jeppson 1970). Croft (unpublished data) found a California strain of *T. mcgregori* to be highly susceptible to laboratory applications of 0.5 mg/ml sol. of technical azinphosmethyl (96 percent purity) when tested using the slide dip method. This pesticide is the most common insecticide applied in apple orchards of Utah or southern California, and its application undoubtedly contributes to the exclusion of *T. mcgregori* from sprayed orchards in both areas.

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HOST-INDUCED MORPHOLOGICAL VARIATIONS IN THE STRIGEOID TREMATODE *POSTHODIPLOSTOMUM MINIMUM* (TREMATODA: DIPLOSTOMATIDAE). III. ORGANS OF ATTACHMENT

James R. Palmieri[1]

Abstract.— A variety of amphibian, reptilian, avian, and mammalian hosts were used in experimental development of *Posthodiplostomum minimum.* As a result of this study much host-induced morphological variation was noted in several organs of attachment. Variations in the oral sucker ranged from a well-developed muscular organ to a weakly developed oral slit. Acetabular development ranged from well-developed to reduced forms lacking apical musculature, tegumental spines, and sensory structures. The holdfast organ showed marked reduction in most poikilothermic hosts.

Members of the family Diplostomatidae Poirier, 1886, constitute a group of trematodes characterized by a distinct flat or spoon-shaped forebody containing an oral sucker, acetabulum, and bulbous tribocytic or holdfast organ. Throughout the literature, when investigators describe strigeoid trematodes, measurements of the oral sucker, acetabulum, and holdfast organ are characteristically given. Little emphasis has been placed on the effects of the definitive host upon the development of these organs.

A variety of amphibian, reptilian, avian, and mammalian hosts were experimentally employed in the development of adult *Postodiplostomum minimum*, a strigeoid trematode characteristically found in a variety of piscivorous avian hosts (Palmieri 1975). As a result of these experimental studies, great variations in the size, shape, and complexity of the oral sucker, acetabulum, and holdfast organ were recorded and are subsequently described in this paper.

Material and Methods

The experimental hosts employed and the techniques used in experimental infections of *P. minimum* to these hosts, as well as specimen preparation for examination by scanning electron microscopy, are explained in detail in part II of this study.

Results and Discussion

Oral sucker.— Five variables were analyzed for the oral sucker of *P. minimum.* (length, width, cross sectional area, ratio of length to width, and ratio of oral sucker-acetabulum cross sectional areas) and are listed in Table 1. Various morphological modifications of the oral sucker are compared according to hosts (Fig. 1-6).

Of all the morphological features of the adult worm examined during this investigation, the oral sucker shows the greatest amount of morphological variation.

In ecologically normal definitive hosts (piscivorous birds), as well as mammalian hosts, the oral sucker is well developed, muscular, and situated in the anteromost portion of the forebody (Figs. 5-8, 14). In certain avian and mammalian hosts, however, it appears to lie below the surface of the anterior end of the forebody (Figs. 3-4, 9-11, 15). In such instances, the cavity of the oral sucker appears collapsed, although the musculature retains its identity. In amphibian and reptilian definitive hosts, an oral sucker appears to be lacking or may be so markedly reduced that only an oral slit appears (Figs. 1-2, 11-13). In cases where the oral slit is present, it does lead into the pharynx. In other than avian hosts, it is not atypical to find some specimens with well-

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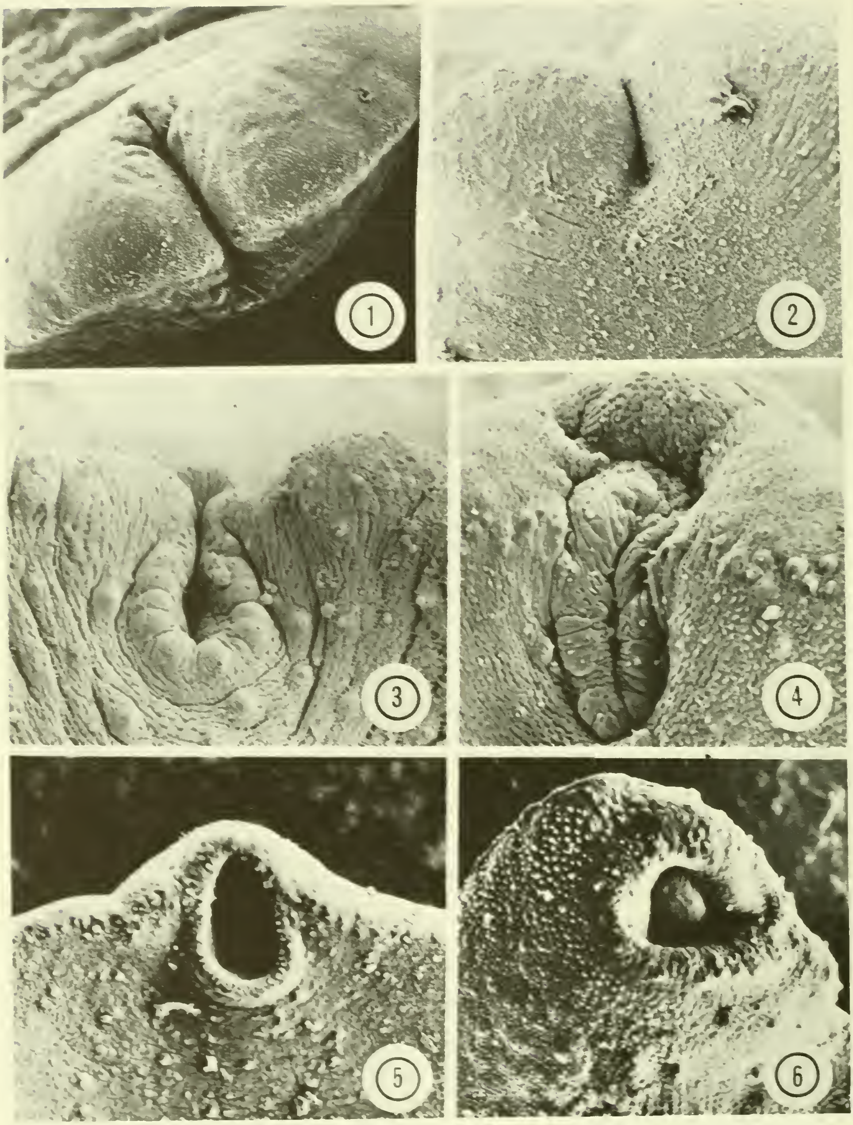


Figs. 1-6. Morphological variations of the oral sucker of adult *P. minimum* from vertebrate hosts. All specimens 72 hours old. (Scale 1 inch = .030 mm) 1, Host: *Bufo americanus*, note presence of an oral slit; 2, Host: *Rana pipiens*, note presence of an oral slit; 3-4, Host: *Iguana iguana*, note the infolding of the oral sucker; 5, Host: *Columba livia*, note the well-developed oral sucker; 6, Host, *Felis catus*, note the well-developed oral sucker.

developed oral suckers and others with oral slits, even among worms recovered from a single definitive host.

ACETABULUM.— Six variables were analyzed in studying the acetabulum (length, width, cross sectional area, ratio of the length to width, acetabular index, ratio of the acetabulum length to the body length, and the acetabulum width to the body width). Length and width were measured along the major axes of the body.

An analysis of the above data appears in Table 2. Morphological variations of the acetabulum are illustrated in Figures 16-21.

Throughout the four classes of definitive hosts experimentally used for development of adult *P. minimum*, complexity in structure and overall size of the acetabulum vary greatly depending on the group of definitive host used. Within some hosts (especially avian) the acetabulum is large, consisting of a full base well endowed with tegumental spines and an expanded muscular surface region covered with two rows of presumed sensory structures. Two views of the acetabulum recovered from the avian host *Larus argentatus* clearly show the above structures (Figs. 18-19). In other hosts, the acetabulum is reduced in size (Fig. 21) and neither the base nor the apical region are fully developed (Figs. 17-25). In one specimen of *P. minimum* recovered from a frog (*Rana pipiens*) (Fig. 16), the base of the acetabulum is not distinguishable, and there is no evidence of apical musculature, well-developed tegumental spination, or sensory structures. In a few abnormally developed worms recovered from *Ambystoma tigrinum*, the acetabulum has apparently degenerated to a point where it is no longer present.

HOLDFAST OR TRIBOCYTIC ORGAN.— Four variables (length, width, cross sectional area, and ratio of length to width) were analyzed in studying the holdfast organ of *P. minimum*. An evaluation of the above data is presented in Table 3. Structure of the holdfast organ is shown on Figures 22-27.

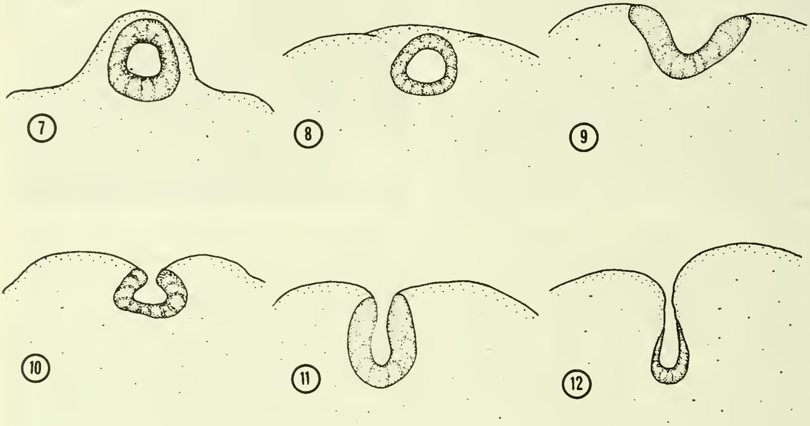
The holdfast or tribocytic organ of *P. minimum* occupies a large portion of the

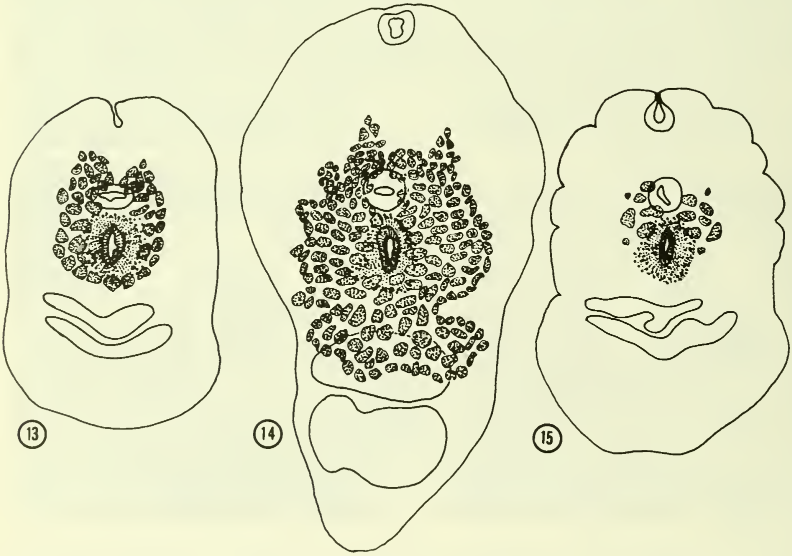
TABLE 1. Statistical analysis of oral sucker measurements of *P. Minimum* from experimental definitive hosts.*

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Oral Sucker Length (OSL)	0.033	0.010	0.029	0.049	0.038	0.036
Oral Sucker Width (OSW)	0.028	0.009	0.026	0.025	0.031	0.029
Cross-sectional Area of Oral Sucker (AOSLYOSW)	0.001	0.001	0.001	0.001	0.001	0.001
Ratio of Oral Sucker Length to Width (ROSLOSW)	1.109	0.393	1.045	0.946	1.232	1.244
Ratio of Oral Sucker to Acetabulum Cross-sectional Area (ROSXXA)	0.524	1.552	0.684	0.388	0.429	0.371

*All measurements in mm.

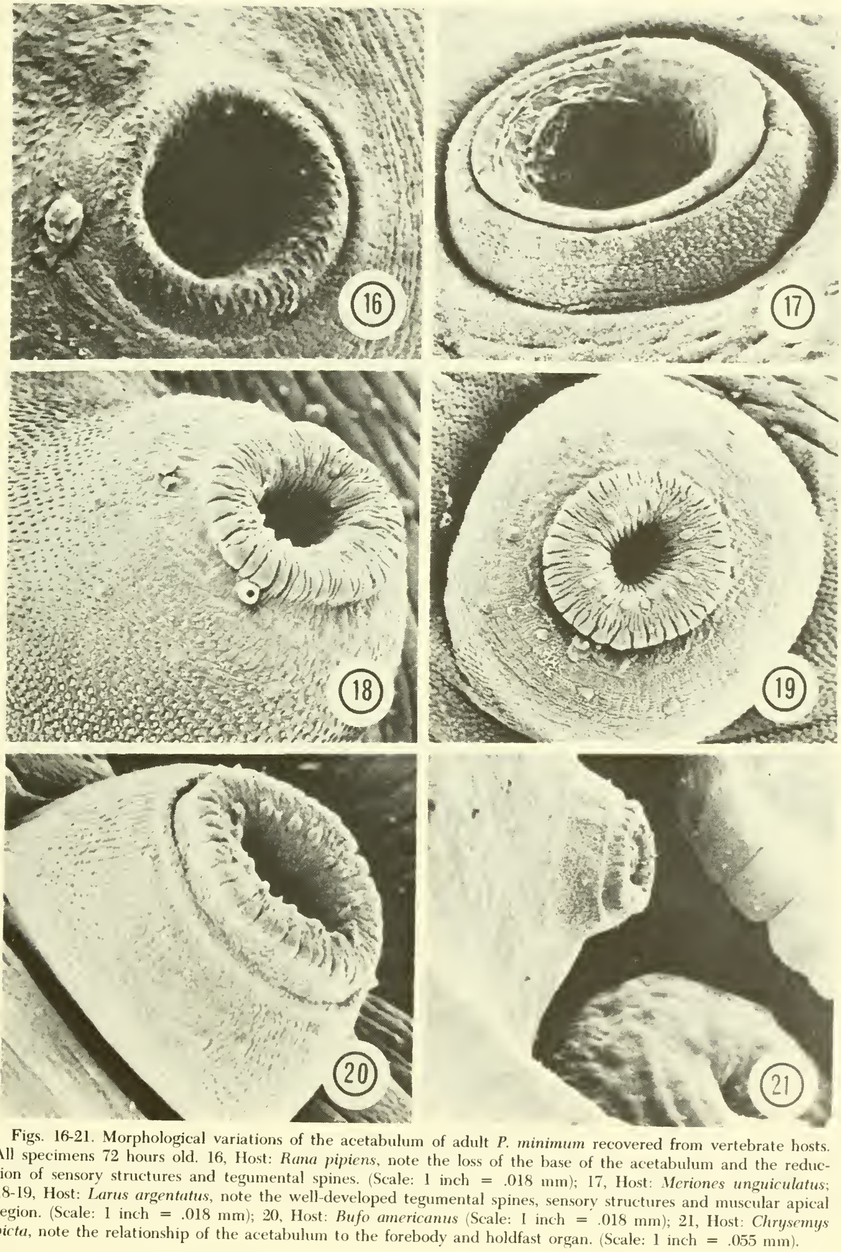
posterior region of the forebody. Although its size is consistent in specimens recovered from most vertebrate hosts, it is somewhat reduced in amphibian and reptilian hosts. The relative constancy in size of the holdfast organ in worms from all vertebrate hosts make variations in the shape of this structure difficult to ascertain. Furthermore, the shape of the holdfast is probably affected by the underlying musculature.



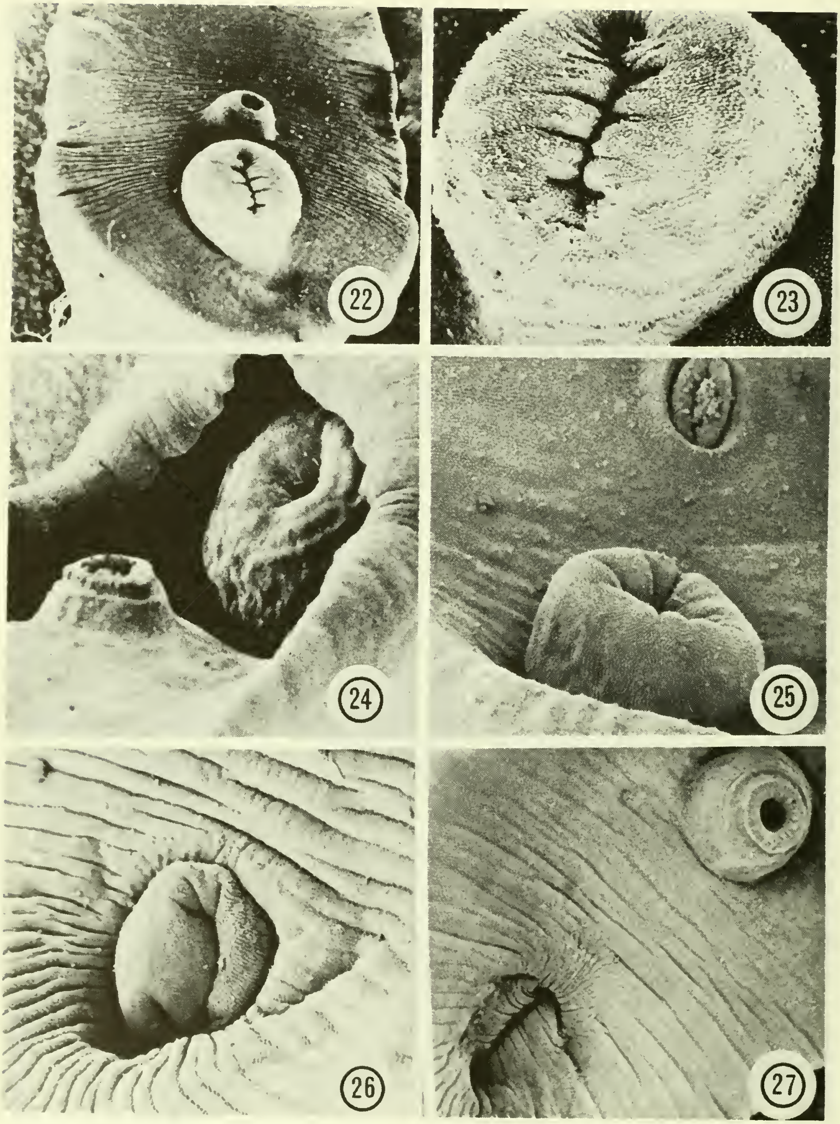


Figs. 7-12. Morphological variations of the oral sucker depicting the normally developed oral sucker and its reduction to an oral slit.

Figs. 13-15. Morphological variations of the oral sucker, vitelline gland, and testes.



Figs. 16-21. Morphological variations of the acetabulum of adult *P. minimum* recovered from vertebrate hosts. All specimens 72 hours old. 16, Host: *Rana pipiens*, note the loss of the base of the acetabulum and the reduction of sensory structures and tegumental spines. (Scale: 1 inch = .018 mm); 17, Host: *Meriones unguiculatus*; 18-19, Host: *Larus argentatus*, note the well-developed tegumental spines, sensory structures and muscular apical region. (Scale: 1 inch = .018 mm); 20, Host: *Bufo americanus* (Scale: 1 inch = .018 mm); 21, Host: *Chrysemys picta*, note the relationship of the acetabulum to the forebody and holdfast organ. (Scale: 1 inch = .055 mm).



Figs. 22-27. Morphological variation of the holdfast (tribocytic organ) of adult *P. minimum*. All specimens 72 hours old. 22-23, Host: *Felis catus*, note large well-developed holdfast; 24-25, Host: *Chrysemys picta*, two views of the holdfast and acetabulum, note the well-developed tegumental spination (Fig. 25); 26, Host: *Canis familiaris*, note the effects of the underlying musculature on the shape of the holdfast; 27, Host: *Meriones unguiculatus*, note the contracted appearance of the holdfast.

TABLE 2. Statistical analysis of acetabulum measurements of *P. Minimum* from experimental definitive hosts.°

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Acetabulum Length (AL)	0.047	0.009	0.046	0.049	0.049	0.047
Acetabulum Width (AW)	0.054	0.010	0.050	0.050	0.060	0.058
Cross-sectional Area of Acetabulum (AALYAX)	0.003	0.001	0.002	0.002	0.002	0.002
Ratio of Acetabulum Length to Width (RALAW)	0.888	0.193	0.929	0.969	0.832	0.794
Acetabulum Index of Length (ACEINDL)	0.095	0.024	0.090	0.142	0.083	0.081
Acetabulum Index of Width (ACEINDW)	0.205	0.045	0.191	0.237	0.212	0.202
Ratio of Oral Sucker Cross-sectional Area to Acetabulum Cross-sectional Area (ROSXXA)	0,524	1.552	0.684	0.388	0.429	0.371

TABLE 3. Statistical analysis of holdfast organ measurements of *P. Minimum* from experimental definitive hosts.°

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Holdfast Length (HL)	0.090	0.018	0.087	0.060	0.106	0.104
Holdfast Width (HW)	0.106	0.019	0.104	0.072	0.127	0.116
Cross-sectional Area of Holdfast (AHLXHW)	0.010	0.003	0.009	0.005	0.014	0.012
Ratio of Holdfast Length to Width (RHLHW)	0.841	0.245	0.854	0.672	0.872	0.912

°All measurements in mm.

Figures 22-23 show the appearance of the holdfast organ in the extended appearance, whereas Figures 26-27 demonstrate the holdfast organ being pulled inward by the underlying musculature.

Examination of the holdfast organ shows that it is well endowed with tegumental spines (Fig. 25). Such spines do not vary appreciably in size and shape as do tegumental spines from other body regions, as reported in part II of this study.

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART V[1]

Stephen L. Wood[2]

ABSTRACT.— New synonymy of American Scolytidae is proposed as follows: *Phloeoborus* Erichson (=*Phloeotrupes* Erichson), *Phloeotribus* Latreille (=*Eulytocerus* Blandford), *Scolytodes* Ferrari (=*Epomadius* Blandford), *Carphoborus pinicolens* Wood (=*Carphoborus tuberculatus* Bright), *Coccotrypes indicus* (Eggers) (=*Dryocoetes subimpressus* Eggers), *Coccotrypes surinamensis* Schedl (=*Coccotrypes brevipilosus* Eggers), *Conophthorus coniperda* Schwarz (=*Conophthorus clunicus* Hopkins, *Conophthorus taedae* Hopkins), *Conophthorus ponderosae* Hopkins (=*Conophthorus scopulorum* Hopkins, *Conophthorus contortae* Hopkins, *Conophthorus monticolae* Hopkins, *Conophthorus flexilis* Hopkins, *Conophthorus lambertianae* Hopkins), *Conophthorus resinosae* Hopkins (=*Conophthorus virginianae* Hopkins), *Cryphalomorphus knabi* (Hopkins) (=*Cryphalomorphus minutissimus* Schedl), *Ips grandicollis* (Eichhoff) (=*Tomicus cribricollis* Eichhoff), *Ips perturbatus* (Eichhoff) (=*Tomicus interpunctus* Eichhoff), *Ips tridens engelmanni* Swaine (=*Ips yohoensis* Swaine, *Ips semirostris* Hopping, *Ips amiskwiensis* Hopping), *Leperisinus aculeatus* (Say) (=*Hylesinus imperialis* Eichhoff), *Leperisinus californicus* Swaine (=*Leperisinus hoferi* Blackman), *Phloeosinus serratus* (LeConte) (=*Phloeosinus neotropicus* Schedl), *Phoeotribus championi* (Blandford))=*Eulytocerus substriatus* Schedl), *Pseudohylesinus sericeus* (Mannerheim) (=*Pseudohylesinus yasamatsui* Nobuchi), *Pityophthorus boycei* Swaine (=*Pityophthorus siouxensis* Bright), *Pityophthorus deletus* LeConte (=*Pityophthorus inquietus* Blackman, *Pityophthorus monophyllae* Blackman, *Pityophthorus praelatus* Bright, *Pityophthorus brucki* Bright), *Scolytus opacus* Blackman (=*Scolytus abietis* Blackman), *Scolytus tsugae* Swaine (=*Scolytus reflexus* Blackman, *Scolytus wickhami* Blackman), *Scolytus unispinosus* LeConte (=*Scolytus fiskei* Blackman). The following species are named as new to science: *Phloeotribus hirtus, P. ingae, P. levis, P. minor, P. nebulosus, P. simplicidens* (Colombia), *P. amplus, P. fici, P. squamiger, P. tetricus, P. vesculus* (Venezuela), *Pityophthorus discretus* (Mexico).

On the following pages several newly discovered cases of synonymy and species new to science are presented for American Scolytidae. The species new to science represent the genera *Phloeotribus* (12) and *Pityophthorus* (1). They are from Mexico (1), Colombia (7), and Venezuela (5).

NEW SYNONYMY

Phloeoborus Erichson

Phloeoborus Erichson, 1836, Arch. Naturgesch. 2(1): 54 (Type-species: *Phloeoborus rudis* Erichson, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48: 126).

Phloeotrupes Erichson, 1836, Arch. Naturgesch. 2(1): 53 (Type-species: *Phloeotrupes grandis*, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48: 127). *New synonymy*

The holotype and 21 other specimens of *Phloeoborus rudis* Erichson, the holotype and two other specimens of *Phloeotrupes grandis* Erichson, and 10 other species in this complex were examined and compared to one another. The characters of the tibiae, antennae, and palpi on which the separation of genera was based, are so variable that no combination of them will distinguish genera. I propose that they be placed in synonymy. Although the name *Phloeotrupes* has page priority, I exercise the option of the first revisor and select *Phloeoborus* as the valid name for the genus, because it is much more widely known in the literature and has been applied to a much larger number of species.

Phloeotribus Latreille

Phloeotribus Latreille, 1796, Précis des caractères génériques des insects, p. 50 (Type-species: *Hylesinus oleae* Fabricius =*Scolytus scarabaeoides* Bernard, subsequent inclusion by Latreille, 1802/3, Histoire naturelle, generale et particulaere des Crustacés et des Insects 3: 203; spelling emendation from *Phloiotribus*, Latreille, 1804, Mag. f. Insekenk. 3: 108)

Eulytocerus Blandford, 1897, Biol. Centr. Amer., Coleopt. 4(6): 161 (Type-species: *Eulytocerus championi* Blandford, monobasic). *New synonymy*

The holotype of *Eulytocerus championi* Blandford was examined and was found to be congeneric with *Phloeotribus* Latreille. All characters of apparent generic value in *championi* are shared by most species of *Phloeotribus.*

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[2] Life Science Museum and Department of Zoology, Brigham Young University, Provo, Utah 84602. Scolytidae contribution no. 65.

Scolytodes Ferrari

Scolytodes Ferrari, 1867, Die Forst- und Baumzuchtschädlichen Borkenkäfer, p. 77 (Type-species: *Scolytodes laevigatus* Ferrari, monobasic)

Epomadius Blandford, 1897, Biol. Centr. Amer., Coleopt. 4(6): 179 (Type-species: *Epomadius culcitatus* Blandford, monobasic). *New synonymy*

Both female syntypes of *Epomadius culcitatus* Blandford were examined. The only unique character on which the genus *Epomadius* was based was the conspicuous pilose impression on each side of the prothorax. There are no other significant characters that separate this species from *Scolytodes.* While the species *culcitatus* is unique, it must be transferred to *Scolytodes* where allied species are placed.

Carphoborus pinicolens Wood

Carphoborus pinicolens Wood, 1954, Canadian Ent. 85: 512 (Holotype, female; Logan Dry Canyon, Utah; U.S. Nat. Mus.)

Carphoborus tuberculatus Bright, 1964, Pan Pacific Ent. 40: 165 (Holotype, female; Crooked Creek, White Mts., Mono Co., California; California Acad. Sci.). *New synonymy*

The large type series of *Carphoborus pinicolens* Wood and the holotype and 48 paratypes of *C. tuberculatus* Bright were examined and compared to one another. The tubercle at the center of the frons in *tuberculatus* is represented in only 77 percent of the females in the type series; it is also present in 70 percent of the females in the type series of *pinicolens.* For this reason, because no other characters distinguish these populations, and since there is continuous distribution between the type localities of this widely distributed species, Bright's name must be placed in synonymy.

Coccotrypes indicus (Eggers)

Thamnurgides indicus Eggers, 1936, Ann. Mag. Nat. Hist. (10)17: 631 (Holotype, female; Sakalaspur, Mysore, India; British Mus. Nat. Hist.)

Dryocoetes subimpressus Eggers, 1940, Arb. Morph. Tax. Ent. Berlin-Dahlem 7: 127 (Holotype, female; Trois Rivières, Guadeloupe; deposited in Eggers Collection, apparently on loan to Schedl). *New synonymy*

The holotype of *Dryocoetes subimpressus* Eggers is a female of *indicus* (Eggers) having a normal head, prothorax, the lateral parts of the elytra, and ventral parts. The median areas of the elytral disc and declivity have the interstriae and spaces between the strial punctures in each row abnormally roughened and distorted. The distortion is similar to that seen in specimens injured by siblings during the pupal stage. Since this is an aberration of a recognizable common species, the name *subimpressus* must be placed in synonymy.

Coccotrypes surinamensis Schedl

Coccotrypes surinamensis Schedl, 1949 (1948), Tijdscr. Ent. 91: 116 (Syntypes; Surinam; Zool. Mus. Amsterdam and Schedl Coll.)

Coccotrypes brevipilosus Eggers, 1951, Ent. Blatt. 45-46: 150 (Holotype, female; Blumenau, Brazil; deposited in Eggers Coll., presumably on loan to Schedl). *New synonymy*

Four specimens, presumably syntypes, of *Coccotrypes surinamensis* Schedl exhibit variability in length of the interstrial setae from very short to normal length for this genus. In one of the specimens these setae, although a bit less consistent in length, are almost indentical to the very short setae on the holotype of *C. brevipilosus* Eggers. Two of the specimens are intermediate between *brevipilosus* and *C. surinamensis* and the fourth specimen is virtually indistinguishable from *surinamensis.* Since virtually all American *Coccotrypes* are known to have been introduced from Africa or the Indo-Australian region, it is very likely that the suspected synonymy with *sundaensis* (Eggers, 1923) will be established as soon as adequate material is available for study. The entire genus *Coccotrypes* is in a state of taxonomic chaos because so many "species" have been named from extraterritorial (introduced) populations without any apparent attempt to establish their origins that identification of most of them is virtually impossible.

Conophthorus coniperda (Schwarz)

Pityophthorus coniperda Schwarz, 1895, Proc. Ent. Soc. Washington (Lectotype, male; Marquette, Michigan; U.S. Nat. Mus., present designation)

Conophthorus clunicus Hopkins, 1915, J. Washington Acad. Sci. 5: 432 (Holotype, female; 13, 122, *To-*

micus clunicus Fitch, Det. No. 12 Hopk., Collection Fitch; U.S. Nat. Mus.). *New synonymy*

Conophthorus taedae Hopkins, 1915, J. Washington Acad. Sci. 5: 431 (Holotype, sex?; Ft. Monroe, Va.; U.S. Nat. Mus.). *New synonymy*

Of the three syntypes of *Pityophthorus coniperda* Schwarz examined at the U.S. National Museum, two are from Marquette and one is from Eagle Harbor, Michigan. I here designate a male syntype from Marquette as the lectotype of *Pityophthorus coniperda* Schwarz. These three syntypes were compared to the holotypes of *C. clunicus* Hopkins and *C. taedae* Hopkins and to 113 other specimens. Only one species is represented by this material. The smaller size, steeper elytral declivity, tuberculate declivital interstriae 1, and other characters clearly distinguish it from the allied *resinosae* Hopkins.

Conophthorus ponderosae Hopkins

Conophthorus ponderosae Hopkins, 1915, J. Washington Acad. Sci. 5: 431 (Holotype, female; Ashland, Oregon; U.S. Nat. Mus.)

Conophthorus scopulorum Hopkins, 1915, J. Washington Acad. Sci. 5: 431 (Holotype, female; Flagstaff, Arizona; U.S. Nat. Mus.). *New synonymy*

Conophthorus contortae Hopkins, 1915, J. Washington Acad. Sci. 5: 432 (Holotype, female; Newport, Oregon; U.S. Nat. Mus.). *New synonymy*

Conophthorus monticolae Hopkins, 1915, J. Washington Acad. Sci. 5: 432 (Holotype, female; Priest River, Idaho; U.S. Nat. Mus.). *New synonymy*

Conophthorus flexilis Hopkins, 1915, J. Washington Acad. Sci. 5: 433 (Holotype female; Mount Manitou, Colorado; U.S. Nat. Mus.). *New synonymy*

Conophthorus lambertianae Hopkins, 1915, J. Washington Acad. Sci. 5: 433 (Holotype, female; Hilt, California; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Conophthorus ponderosae* Hopkins, *C. scopulorum* Hopkins, *C. contortae* Hopkins, *C. monticolae* Hopkins, *C. flexilis* Hopkins, and *C. lambertianae* Hopkins were compared directly to one another and studied in conjunction with 784 other specimens. Although a limited amount of variability occurs in all series, I see no basis for recognizing more than one species from this material. Because the name *ponderosae* has been used more widely in the literature, it was selected to designate this species. In view of the sibling species *resinosae* and *banksianae* that are distinguishable only from their habits there is a possibility that sibling species occur in the material treated here as *ponderosae.* Extensive biological work will be required to determine whether or not this is the case.

Conophthorus resinosae Hopkins

Conophthorus resinosae Hopkins, 1915, J. Washington Acad. Sci. 5: 431 (Holotype, male; Conoph. resinosae Hopkins, 1 Harring., *Conophthorus resinosae;* U.S. Nat. Mus.)

Conophthorus virginianae Hopkins, 1915, J. Washington Acad. Sci. 5: 431 (Holotype, male, not a female as labeled; Huttonsville, West Virginia; U.S. Nat. Mus.). *New synonymy*

The male holotypes of *Conophthorus resinosae* Hopkins and *C. virginianae* Hopkins were compared directly to one another and were studied with 166 other specimens. Although minor variation exists in this material, only one species is represented. It is distinguished from the allied *C. coniperda* (Schwarz) by characters listed above under that species. Except for size and host I see no means of distinguishing it from *C. banksianae* McPherson, although both appear to be valid species.

Cryphalomorphus knabi (Hopkins)

Ernoporides knabi Hopkins, 1915, Dept. Agric. Rept. 99: 34 (Holotype, female; Cordoba, Mexico; U.S. Nat. Mus.)

Cryphalomorphus minutissimus Schedl, 1951, Dusenia 2: 97 (Holotype male; Env. de Trois Rivières, Guadeloupe; Schedl Coll.). *New synonymy*

The male holotype of *Cryphalomorphus minutissimus* Schedl is somewhat smaller than average for the species and the basal half of the elytra have been rubbed, but there is no doubt that it represents *C. knabi* (Hopkins), a very common and widely distributed species in the Caribbean region. The type of *minutissimus* when received on loan for study had fallen from its mount and was crushed between the wall and pinning surface of the shipping box. The fragments were recovered and re-mounted by me; no other possible contaminating parts were in the box.

Ips grandicollis (Eichhoff)

Tomicus grandicollis Eichhoff, 1868, Berliner Ent. Zeitschr. 11: 402 (Syntypes; Amerique boreali; presumably lost with Hamburg Mus.)

Tomicus cribricollis Eichhoff, 1869, Berliner Ent.

Zeitschr. 12: 273 (Holotype, male; Mexico; Brussels Mus.). *New synonymy*

This species is easily recognized from the description, although the type series of *Tomicus grandicollis* Eichhoff is lost. More than 1,000 specimens from the United States and eastern Canada were examined in addition to the holotype of *Tomicus cribricollis* Eichhoff and about 500 specimens from Mexico and Central America. Although geographical variation is apparent, it does not appear to be correlated with characters reported by Lanier (1970, Canadian Ent. 102: 1151) nor can I confirm all of the characters he used to distinguish *grandicollis* and *cribricollis.* Until a more comprehensive analysis can be made, *cribricollis* should be regarded as a junior synonym of *grandicollis.*

Ips perturbatus (Eichhoff)

Tomicus perturbatus Eichhoff, 1869, Berliner Ent. Zeitschr. 12: 274 (Syntypes?; Amerique boreali; presumably lost with Hamburg Mus.)

Tomicus interpunctus Eichhoff, 1878, preprint of Mém. Soc. Roy. Sci. Liége (2)8: 241 (Syntypes?; Sitka, Alaska; presumably lost with Hamburg Mus.). *New synonymy*

The type series of both *Tomicus perturbatus* Eichhoff and *T. interpunctus* Eichhoff were lost when the Hamburg Museum was destroyed. Prior to that time Eichhoff had examined part of the original series of *T. hudsonicus* LeConte and referred them to *perturbatus.* The identity of *interpunctus* has not been clarified. According to the original description, *interpunctus* was 4.0 mm long, it had a pair of transversely arranged tubercles near the center of the frons, and the basal parts of the interstriae were impunctate. The only Sitka *Ips* of this size, with paired frontal tubercles and basally impunctate interstriae is *perturbatus.* It is also the most common *Ips* in the Sitka area. Although *pini* (Say) has frontal tubercles in some parts of its range, it does not have them in areas adjacent to Sitka and there are no records of it from Sitka. For these reasons, *interpunctus* is placed in synonymy under *perturbatus.*

Ips tridens engelmanni Swaine

Ips engelmanni Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1): 30 (Lectotype, female; Rogers Pass, British Columbia; Canadian Nat. Coll., designated by Bright, 1967, Canadian Ent. 99: 675)

Ips yohoensis Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1): 31 (Lectotype, female; Yoho Valley, British Columbia; Canadian Nat. Coll. designated by Bright, 1967, Canadian Ent. 99: 676). *New synonymy*

Ips semirostris Hopping, 1963, Canadian Ent. 95: 213 (Holotype, female; Kenai Penninsula, Alaska; Canadian Nat. Coll.). *New synonymy*

Ips amiskwiensis Hopping, 1963, Canadian Ent. 95: 216 (Holotype, female; Amiskwi River Yoho Nat. Pk., British Columbia; Canadian Nat. Coll.). *New synonymy*

The types and most of the type series of *Ips engelmanni* Swaine, *I. yohoensis* Swaine, *I. semirostris* Hopping, and *I. amiskwiensis* Hopping and 580 other specimens of this species were examined and compared. The female frons is unusually variable and appears in forms varying from almost uniformly convex to moderately protuberant to exceedingly protuberant, with or without abundant vestiture. The various forms may appear in pure or mixed series and are known to be morphological expressions of various gene combinations and do not express specific differences.

Leperisinus aculeatus (Say)

Hylesinus aculeatus Say, 1824, J. Acad. Nat. Sci. Philadelphia 3: 322 (Syntypes?; Missouri; evidently lost)

Hylesinus imperialis Eichhoff, 1868, Berliner Ent. Zeitschr. 12: 149 (Syntypes; Wisconsin and Georgia; lost with Hamburg Mus.). *New synonymy*

LeConte's series of *Hylesinus aculeatus* Say was either part of the Say series or was compared to it; his series of *H. imperialis* Eichhoff was either part of Eichhoff's series or was compared to it. Both of LeConte's series are of the same species. The size, descriptions, and distributions are such that there is virtually no question that both names apply to the same species. In view of these facts and since *imperialis* has been a doubtful species since it was first proposed, these names are considered synonymous.

Leperisinus californicus Swaine

Leperisinus californicus Swaine, 1916, Canadian Ent. 48: 190 (Holotype, female; San Diego, California; Canadian Nat. Coll.)

Leperisinus hoferi Blackman, 1943, Proc. U.S. Nat. Mus. 93: 394 (Holotype, female; Sabino Canyon, Arizona; U.S. Nat. Mus.). *New synonymy*

The holotypes of *Leperisinus californicus* Swaine and *L. hoferi* Blackman and 242 other specimens from Oregon and North Dakota to California and Chihuahua were examined and compared. From this material it is apparent that only one species is present. Apparently Blackman was not familiar with Swaine's species when *hoferi* was named.

Phloeosinus serratus LeConte

Hylesinus serratus LeConte, 1868, Trans. Amer. Ent. Soc. 2: 170 (Holotype, male; Middle States; Mus. Comp. Zool.

Phloeosinus neotropicus Schedl, 1939, Proc. Roy. Ent. Soc. London 8(1): 12 (Holotype, female; Jamaica; British Mus. Nat. Hist.). *New synonymy*

The male holotype of *Hylesinus serratus* LeConte was examined and compared to several examples of my specimens. It represents a common species from Washington and Idaho to Durango (Mexico) and Texas. The female holotype of *Phloeosinus neotropicus* Schedl was examined, but, as is the case with many female *Phloeosinus*, it could not be associated with any other material at that time. The male "paratype" in the Schedl collection, however, is an easily diagnosed normal specimen of *serratus*. Once this association was made, the female holotype could then be placed as a synonym of *serratus*. There is doubt as to whether or not this species is established in Jamaica.

Phloeotribus championi (Blandford), n. comb.

Eulytocerus championi Blandford, 1897, Biol. Centr. Amer., Coleopt. 4(6): 161 (Holotype, male; Volcan de Chiriqui, Chiriqui, Panama; British Mus. Nat. Hist.)

Eulytocerus substriatus Schedl, 1935, Rev. de Ent. 5: 344 (Holotype, male; Turrialba, Costa Rica; Schedl Coll.). *New synonymy*

The male holotypes of *Eulytocerus championi* Blandford, length 3.7 m, and *E. substriatus* Schedl, length 3.6 mm, were compared directly to one another. Although the frontal setae of the former are slightly longer and the interstrial punctures of the latter are slightly deeper, the differences appear insignificant. Only one species can be recognized in this material; consequently, Schedl's name is placed in synonymy.

Pseudohylesinus sericeus (Mannerheim)

Hylesinus sericeus Mannerheim, 1843, Bull. Soc. Imp. Nat. Moscou 16(2): 296 (reprint p. 124) (Holotype, female; Alaska; Univ. Zool. Mus., Helsinki)

Pseudohylesinus yasamatsui Nobuchi, 1971, Bull. Gov. For. Expt. Sta., Tokyo 238: 160 (Holotype, male; Takanishi, Nagano, Japan; Gov. For. Expt. Sta., Tokyo). *New synonymy*

Two paratypes of *Pseudohylesinus yasamatsui* Nobuchi in the Canadian National Collection are identical to my series of *sericeus* (Mannerheim) two of which were compared to the holotype at the Helsinki Museum by me. Nobuchi's name therefore, must be placed in synonymy. This is the first reported introduction of a member of this genus outside of western North America.

Pityophthorus boycei Swaine

Pityophthorus boycei Swaine, 1925, Canadian Ent. 57: 192 (Holotype, male; Cisco, Placer Co., California; Canadian Nat. Coll.)

Pityophthorus siouxensis Bright, 1977, Great Basin Nat. 36: 439 (Holotype, female; Black Hills, South Dakota; Canadian Nat. Coll.). *New synonymy*

The type series of *Pityophthorus boycei* Swaine, *P. catulus* Blackman, *P. iniquus* Blackman, and *P. siouxensis* Bright and 133 other specimens from British Columbia and California eastward to South Dakota and Colorado were examined and compared directly to one another. Although slight variation within and between series is evident, it is clear that only one species is represented by this material.

Pityophthorus deletus LeConte

Pityophthorus deletus LeConte, 1879, U.S. Dept. Interior, Geol., Geogr. Surv. Bull. 5: 519 (Lectotype, female; Veta Pass, Colorado; Mus. Comp. Zool., designated by Bright, 1976, Coleopt. Bull. 30: 185)

Pityophthorus inquietus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25: 46 (Holotype, female; Las Vegas Hot Springs, New Mexico; U.S. Nat. Mus.). *New synonymy*

Pityophthorus monophyllae Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25: 47 (Holotype, female; Argus Mts., California; U.S. Nat. Mus.). *New synonymy*

Pityophthorus praelatus Bright, 1966, Pan Pacific Ent.

42: 303 (Holotype, female; Mt. Shasta Ski Area, Siskiyou Co., California; California Acad. Sci.). *New synonymy*

Pityophthorus brucki Bright, 1971, Pan Pacific Ent. 47: 63 (Holotype, female; San Bernardino, California; Ohio State Univ. Coll.). *New synonymy*

Two syntypes of *Pityophthorus deletus* LeConte, the holotypes and most of the type series of *P. inquietus* Blackman, *P. monophyllae* Blackman, and *P. brucki* Bright, and two paratypes of *P. praelatus* Bright, and more than 400 other specimens were studied and compared directly to one another and to examples of my material. Variations in the female frons are conspicuous and are partly associated with geographic origin. The type series of *monophyllae*, from the Argus Mountains, California, and a series from Beaver, Utah contain some females with very long and others with very short or no frontal setae. Series from San Bernardino and Ventura counties, California contained females with the frons very strongly, extensively flattened in various patterns and with long hair in a variety of arrangements. In view of the limited material available from California and the conspicuous variability within and between series in the remainder of the range, from South Dakota to Durango (Mexico) and westward, it is considered advisable to treat all of this material as one species until a comprehensive analysis can be made.

Scolytus opacus Blackman

Scolytus opacus Blackman, 1934, U.S. Dept. Agric. Tech. Bull. 431: 20 (Holotype, male; Ouray, Colorado; U.S. Nat. Mus.)

Scolytus abietis Blackman, 1934, U.S. Dept. Agric. Tech. Bull. 431: 21 (Holotype, male; Sandpoint, Idaho; U.S. Nat. Mus.). *New synonymy*

The male holotypes of *Scolytus opacus* Blackman and *S. abietis* Blackman and more than one hundred other specimens were compared directly to one another. Specimens from the Pacific Coast states and northern Idaho have the spine on male sternum 2 slightly smaller, with the summit more narrowly rounded and its crest acute and with the vertex of the head more strongly convex. Some males from the southern Rocky Mountain area have the summit of the spine on sternum 2 flattened or sulcate and the vertex less strongly convex. Since the types of *opacus* and *abietis* represent the extremes in these characters and because both characters intergrade in series from intermediate localities, it is necessary to place one of the names in synonymy. The name *opacus* was selected as the name to be used for this species.

Scolytus tsugae Swaine

Scolytus tsugae Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1): 32 (Lectotype, female; Glacier, British Columbia; Canadian Nat. Coll., designated by Bright, 1967, Canadian Ent. 99: 674)

Scolytus reflexus Blackman, 1934, U.S. Dept. Agric. Tech. Bull. 431: 13 (Holotype, male; Santa Catalina Mts., Arizona; U.S. Nat. Mus.). *New synonymy*

Scolytus wickhami Blackman, 1934, U.S. Dept. Agric. Tech. Bull. 431: 13 (Holotype, male; Buena Vista, Colorado; U.S. Nat. Mus.). *New synonymy*

In an earlier paper, I (Wood, 1966, Great Basin Nat. 26: 30) placed *Scolytus monticolae* Swaine in *synonymy* under *S. tsugae* Swaine. The examination of the holotypes of *S. reflexus* Blackman and *S. wickhami* Blackman and more than 100 other specimens from eastern Washington and northern Idaho to Arizona leaves little doubt that only one species exists in this area. However, this poulation forms a longitudinal parental gallery, while the coastal form apparently forms a transverse one. The absence of significant morphological characters suggests that only one species is represented by this material and that *reflexus* and *wickhami* must be placed in *synonymy*. The apparent difference in galleries suggests the necessity for a critical reexamination of this species as soon as adequate material for study is available.

Scolytus unispinosus LeConte

Scolytus unispinosus LeConte, 1876, Proc. Amer. Philos. Soc. 15: 372 (Lectotype, male; Oregon; Mus. Comp. Zool., present designation)

Scolytus fiskei Blackman, 1934, U.S. Dept. Agric. Tech. Bull. 431: 25 (Holotype, male; Capitan Mts., New Mexico; U.S. Nat. Mus.). *New synonymy*

The male syntype of *Scolytus unispinosus* in the LeConte collection that is labeled "type" is here designated as the lectotype of LeConte's name *unispinosus*. That lectotype, the holotype of *S. fiskei* Blackman, and 164 other specimens from British Columbia to Arizona were examined. Although slight geographical differences are apparent, individual variation within series is such that it is impossible to recognize geographical races or species. Therefore, *fiskei* must be placed in synonymy under the senior name, *unispinosus*.

New Taxa

Phloeotribus tetricus, n. sp.

This species is distinguished from *venezuelensis* Schedl by the larger average size, by the larger, deeper pronotal punctures, and by differences in the frons, elytra, and vestiture noted below.

Male.— Length 1.8 mm (paratypes 1.7-2.1 mm), 1.8 times as long as wide; color reddish brown.

Frons transversely impressed slightly above level of antennal insertion, convex above, with a large, subfoveate impression on median fourth, lower area shallowly, rather broadly impressed, epistomal margin rather broadly, acutely carinate, carina low, indefinite laterally; surface shining, upper area coarsely punctured, rugose-reticulate in interspaces, lower area reticulate, with a few fine punctures; vestiture inconspicuous. Antenna about as in *venezuelensis*.

Pronotum similar to *venezuelensis* except punctures coarser, deeper, vestiture more slender. Anterolateral areas unarmed in both species.

Elytra similar to *venezuelensis* except strial punctures considerably larger, deeper, interstriae half as wide as striae, tubercles on odd-numbered interstriae larger, high, narrow, pointed, continuing to lower half of declivity, those on even-numbered interstriae obsolete except near base, vestiture more abundant, more slender, a few on central row of each interstriae longer.

Female.— Similar to male except lower half of frons almost flat, carina not clearly evident, transverse impression less conspicuous.

Type Locality.— La Carbonera Experimental Forest, about 50 km (airline) NW Merida, Merida, Venezuela.

Type Material.— The male holotype, female allotype, and 25 paratypes were taken at the type locality on 27-X-1969, 2500 m, No. 93, from the bole of *Eschweilera* sp., by me. Two paratypes were taken at the same locality on 12-I-1970, from a woody vine, by me. The holotype, allotype, and paratypes are in my collection.

Phloeotribus ingae, n. sp.

This species is distinguished from *simplex* Wood by the smaller size, by the absence of reticulation on the pronotum, by the less strongly impressed striae and strial punctures, and by the more slender elytral setae.

Male.— Length 1.5 mm (paratypes 1.4-1.7 mm), 2.0 times as long as wide; color brown.

Frons broadly, deeply concave from epistoma to upper level of eyes, lateral margins subcostate on lower half; surface smooth, shining, punctures small, rather sparse; vestiture short, rather sparse, inconspicuous.

Pronotum as in *simplex* except surface smooth, shagreened, without any reticulation, punctures more sharply, rather shallowly impressed.

Elytra as in *simplex* except surface slightly shagreened, strial punctures slightly smaller, interstriae one and one-half times as wide as striae, interstrial tubercles smaller in diameter, higher, vestiture slightly more slender, of similar length and abundance, strial punctures on declivity much smaller, less strongly impressed.

Female.— Similar to male except frons almost flat on lower half, convex above, punctures moderately coarse, shallow.

Type Locality.— Bugo, Columbia.

Type Material.— The male holotype, female allotype, and 101 paratypes were taken at the type locality on 16-V-1973, from two pods of *Inga* sp., by G. Ekis.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus simplicidens, n. sp.

This species is distinguished from *ingae* Wood by the much more deeply impressed male frons, by the finer punctures and deep median fovea on the female frons, and by other characters described below.

Male.— Length 1.8 mm (paratypes 1.7-

1.9 mm), 2.0 times as long as wide; color yellowish brown.

Frons as in *ingae* except impression distinctly deeper, its surface reticulate.

Pronotum as in *ingae* except surface contour more uniform, punctures slightly larger, deeper.

Elytra as in *ingae* except strial punctures slightly larger, interstrial tubercles smaller, vestiture finer; interstrial tubercles on declivity almost obsolete on lower half.

FEMALE.— Similar to male except frons convex; as in female *ingae* except punctures very small, central area with a large, deep fovea.

TYPE LOCALITY.— Finca La Hermosa, Salento, Caldas, Colombia.

TYPE MATERIAL.— The male holotype, female allotype, and eight paratypes were taken at the type locality on 1-VI-1959, en guamo, by J. A. Garzon.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus amplus, n. sp.

This species apparently represents a unique species group within the genus. It is distinguished by the large size, rather slender form, simple male frons, asperate pronotum and simple elytra. It may be remotely related to the *setulosus* group of species.

MALE.— Length 3.3 mm (paratypes 3.3-3.8 mm), 2.1 times as long as wide; color dark brown.

Frons with a large, strong, median fovea two-thirds distance from epistoma to upper level of eyes, lower area shallowly impressed, smooth, shining, closely, finely punctured, upper area convex, rather coarsely punctured, with a few small, isolated tubercles; vestiture sparse, inconspicuous. Each segment of antennal club about three times as wide as long.

Pronotum 0.8 times as long as wide; widest at base, sides accurately converging toward rather broadly rounded anterior margin; surface shining, rather finely, densely asperate except basal third on median half closely, rather coarsely, deeply punctured. Vestiture short, fine, moderately abundant.

Elytra 1.4 times as long as wide, 2.0 times as long as pronotum; sides straight and parallel on basal two-thirds, rather narrowly rounded behind; striae moderately impressed, punctures coarse, deep, very close; interstriae as wide as striae, shining, uniseriately crenulate except confused near base on 1 and 3, crenulations each half as wide as interstriae, transversely, acutely, moderately elevated, submarginal ones at base larger. Declivity steep, convex; striae and interstriae about half as wide as on disc, crenulations narrower, forming acutely pointed, small tubercles, interstriae 9 slightly elevated, more strongly serrate. Vestiture of uniseriate rows of fine interstrial setae, each seta equal in length to three-fourths distance between rows.

FEMALE.— Similar to male except frons convex, with a distinct transverse impression and a conspicuous median fovea near middle.

TYPE LOCALITY.— La Carbonera Experimental Forest, 50 km (airline) northwest Merida, Merida, Venezuela.

TYPE MATERIAL.— The male holotype, female allotype, and 10 paratypes were taken at the type locality on 14-X-69, 2500 m, No. 59, from the bole of a large unidentified tree, by me.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus nebulosus, n. sp.

Although this species apparently belongs to the *setulosus* group, it lacks an epistomal male carina, the male scape is less densely setose, and declivital interstriae 9 is less strongly elevated than in most representatives of the group.

MALE.— Length 1.9 mm (paratypes 1.7-2.0 mm), 1.9 times as long as wide; color very dark brown, almost black.

Frons shallowly concave from epistoma almost to upper level of eyes, a transverse impression with a median fovea somewhat deeper two-thirds of distance from epistoma to upper level of eyes; epistomal carina not indicated; surface strongly reticulate, a few small, obscure punctures and granules on upper third; vestiture sparse, short, inconspicuous. Antenna about as in *setulosus*

Eichhoff except long setae on scape about one-third as numerous.

Pronotum about as in *setulosus* except asperities smaller, punctures on basal half larger, more clearly impressed, vestiture much finer.

Elytra 1.3 times as long as wide, 1.9 times as long as pronotum; much as in *setulosus* except interstriae slightly impressed at base, moderately impressed on posterior half of disc, punctures coarse, deep; interstriae as wide as striae, crenulations narrower than in *setolosus;* declivital sculpture about as on disc except striae and interstriae slightly narrower, tubercles narrower, pointed; declivital interstriae 9 much less strongly elevated than in *setulosus*, moderately high, rather coarsely, closely tuberculate. Vestiture of uniseriate rows of fine bristles, each slightly shorter than distance between rows.

Female.— Similar to male except frons convex, strongly reticulate, obscure punctures of moderate size indicated, a median fovea slightly above middle.

Type Locality.— Piedras Blancas, 11 km west of Medellin, Antioquia, Colombia.

Type Material.— The male holotype, female allotype, and 126 paratypes were taken at the type locality on 17-VII-1970, 2300 m, No. 693, from *Croton guianensis*, by me.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus minor, n. sp.

This species is distinguished from *armatus* Blandford by the much smaller size and by numerous characters described below.

Male.— Length 1.3 mm (paratypes 1.2-1.4 mm), 2.1 times as long as wide; color very dark brown.

Frons as in *armatus* except less strongly impressed, epistomal carina less strongly elevated.

Pronotum as in *armatus* except sculpture slightly finer.

Elytra as in *armatus* except striae much less strongly impressed, punctures more clearly defined, more distinctly impressed, interstrial crenulations not as high or as coarse, declivital sculpture much finer, interstriae 9 only moderately elevated, much less strongly, less closely serrate, vestiture much finer.

Female.— Similar to male except frons convex, with an indefinite central fovea, surface reticulate, punctures shallow, obscure, moderately coarse; asperities on anterolateral areas of pronotum usually larger; declivital interstriae 2 and 4 sometimes with a few tubercles.

Type Locality.— Twenty-seven km northeast of Montoya, Santander, Colombia.

Type Material.— The male holotype, female allotype, and 36 paratypes were taken at the type locality on 2-VII-1970, 150 m, No. 601, from a *Pseudoolmedia* limb, by me. *Cladoctonus boliviae* Wood was using the entrance tunnels of this species to gain access to the cambium region.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus remorsus, n. sp.

This species is distinguished from *setulosus* Eichhoff by the much larger size, by the dull, uniformly, strongly reticulate pronotum, and by other characters described below.

Male.— Length 2.9 mm (paratypes 2.4-3.2 mm), 1.7 times as long as wide; color dark brown.

Frons as in *setulosus* except slightly higher, slightly narrower, reticulation more uniform more strongly impressed.

Pronotum as in *setulosus* except surface dull, uniformly, strongly reticulate, punctures very small, inconspicuous.

Elytra as in *setulosus* except strial punctures smaller, less sharply defined, declivital tubercles on interstriae 3, 5, and 7 slightly larger, almost obsolete on 6 and 8, 9 more acutely elevated.

Female.— Similar to male except irregularly convex, uniformly, strongly reticulate, punctures and central fovea obscure; anterolateral crenulations on pronotum larger.

Type Locality.— Piedras Blancas, 10 km east Medellin, Antioquia, Colombia.

Type Material.— The male holotype, female allotype, and 80 paratypes were taken at the type locality on 15-VII-1970, 2500 m, No. 654, from a *Quercus humboldtii* branch, by me.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus vesculus, n. sp.

This species may be remotely allied to *squamatus* Wood, but it is distinguished by the stouter body form, by the obscure lateral asperities on the pronotum, and by other characters described below.

FEMALE.— Length 1.3 mm, 1.9 times as long as wide; color very dark brown.

Frons convex, strongly reticulate, a pair of calluses on median two-thirds slightly above level of antennal insertion. Segments of antennal club slightly more than twice as wide as long.

Pronotum about as in *squamatus* except anterior constriction obsolete, a few obscure crenulations in lateral areas; surface uniformly reticulate, punctures very shallow, coarse. Setae short, coarse, each widest on its distal half.

Elytra 1.2 times as long as wide, 1.6 times as long as pronotum; sides straight and parallel on basal two-thirds, very broadly rounded behind; striae not impressed except 1 weakly, punctures coarse moderately deep, close; interstriae slightly narrower than striae, shining, with moderately abundant fine, confused punctures, each with a uniseriate row of pointed tubercles, tubercles spaced by distance equal to width of an interstriae. Declivity very steep convex; striae and interstriae narrower than on disc; tubercles obsolete on interstriae 1 and 2. Vestiture consisting of interstrial rows of erect bristles; each bristle stout, widest on its distal half, about six times as long as wide, about two-thirds as long as distance between rows.

TYPE LOCALITY.— Five km west of El Pino, Zulia, Venezuela.

TYPE MATERIAL.— The female holotype was taken at the type locality on 20-X-1969, 10 m, No. 140, from an *Ochroma* branch, by me.

The holotype is in my collection.

Phloeotribus levis, n. sp.

This species apparently is distantly allied to *squamatus* Wood but is distinguished by the impressed striae, slender interstrial setae, and many other characters.

MALE.— Length 1.5 mm (paratypes 1.7 mm), 2.1 times as long as wide; color very dark brown.

Frons moderately concave from epistoma to upper level of eyes, sulcus narrower and deeper near middle, lateral margins and epistoma not elevated or armed; surface reticulate, obscurely so on lower half; vestiture short, fine, sparse. Segments of antennal club about four times as wide as long.

Pronotum about as in *squamatus* except surface reticulate, punctures moderately coarse, sharply, shallowly impressed, spaced by one-half to three diameters of a puncture. Vestiture of fine, short, inconspicuous hairlike setae.

Elytral outline about as in *squamatus;* striae impressed, moderately near base, rather strongly near declivity, punctures rather coarse, deep, close; interstriae as wide as striae, rather strongly convex, smooth and shining, each armed by a uniseriate row of moderately high crenulations, each crenulation about two-thirds as wide as interstriae, crenulations spaced in row by distance slightly less than width of an interstriae. Declivity steep, convex; sculpture about as on disc except striae and interstriae distinctly narrower, crenulations narrowed to become rounded tubercles except slightly larger on interstriae 9. Vestiture of interstrial rows of slender setae each as long as distance between rows, much stouter (8-10 times as long as wide) on declivity.

FEMALE.— Similar to male except frons convex, an obscure, shallow median fovea at center, punctures rather sparse, moderately coarse declivital setae not as stout.

TYPE LOCALITY.— Piedras Blancas, 10 km east of Medellin, Antioquia, Colombia.

TYPE MATERIAL.— The male holotype, female allotype, and one female paratype were taken at the type locality on 15-VII-1970, 2500 m, No. 658, from a branch of a tree known locally as Graptero, by me.

The holotype, allotype, and paratype are in my collection.

Phloeotribus squamiger, n. sp.

This species is distinguished from *squam-*

atus Wood by the larger size and by numerous minor characters described below.

MALE.— Length 1.5 mm (paratypes 1.4-1.7 mm), 2.1 times as long as wide; color black with white setae.

Frons as in *squamatus* except slightly more strongly, more uniformly concave, median epistomal tubercle much narrower, slightly higher.

Pronotum as in *squamatus* except shallow punctures more clearly impressed, scales stouter.

Elytra as in *squamatus* except strial punctures evidently slightly larger, scales in interstrial rows stouter, each almost as wide as long.

FEMALE.— Similar to male except frons convex, strongly reticulate, with a few minute granules.

TYPE LOCALITY.— Colonia Tovar, Aragua, Venezuela.

TYPE MATERIAL.— The male holotype, female allotype, and 30 paratypes were taken at the type locality on 4-V-1970, 1700 m, No. 495a, from *Inga* branches, by me. Two paratypes are from La Carbonera Experimental Forest near Merida, Merida, Venezuela, 27-X-1969, 2500 m, No. 89, from a tree seedling, by me.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus hirtus, n. sp.

This species is distinguished from *spinipennis* Eggers by the smaller size, by the unarmed lateral margins of the male frons, by the more coarsely punctured pronotum, and by the very different declivity and vestiture.

MALE.— Length 2.0 mm (paratypes 1.9-2.1 mm), 2.0 times as long as wide; color very dark brown to almost black.

Frons moderately, broadly concave from epistoma to upper level of eyes, lateral margins moderately elevated, unarmed; surface smooth, shining, a few, fine punctures and granules evident; vestiture fine, sparse, inconspicuous. Antennal scape with a small tuft of hair; segments of club about six times as wide as long.

Pronotum shape about as in *spinipennis;* basal half very coarsely, closely, deeply punctured, interspaces smooth, shining, without micropunctures, asperities on anterolateral areas very small, obscure. Vestiture of moderately long, fine hair.

Elytra 1.4 times as long as wide, 1.8 times as long as pronotum; outline about as in *spinipennis;* striae moderately impressed, punctures coarse, deep, close; interstriae as wide as striae, rather strongly convex, smooth shining, tubercles uniseriate, rather small except one or two near margin of declivity rather coarse. Declivity steep, convex; sculpture much as on declivity except striae and interstriae slightly narrower, strial punctures half as large; most interstrial tubercles replaced by punctures, a rather coarse tubercle at base on 3, 5, and 7, at middle on 3 and near apex on 1, 9 acutely, rather strongly elevated and coarsely serrate. Vestiture of slender, erect interstrial hair, each seta at base twice as long as distance between rows, up to four times as long at base of declivity, slightly shorter on lower declivity.

FEMALE.— Similar to male except frons convex, median fovea indefinite, surface strongly reticulate, rather coarsely, closely punctured; tuft of hair on scape absent; setae on elytra slightly shorter.

TYPE LOCALITY.— Caparrapi, Cunadin, Colombia.

TYPE MATERIAL.— The male holotype, female allotype, and eight paratypes were taken at the type locality on 28-V-1959, from Arbol de Sangregao, by A. Diaz.

The holotype, allotype, and paratypes are in my collection.

Phloeotribus fici, n. sp.

This species is distinguished from *hirtus* Wood by the smaller size, by the more shallowly impressed frons, by the shorter elytral setae, and by the coarser declivital tubercles.

MALE.— Length 1.6 mm, 2.0 times as long as wide; color black.

Frons shallowly impressed, almost flat, from epistoma to upper level of eyes, lateral margins weakly elevated at level of antennal insertions, an elongate fovea at middle; surface reticulate, punctures moderately fine, not close, about uniformly distributed; vestiture fine, short, inconspicuous.

Pronotum about as in *hirtus* except punctures larger, asperities almost obsolete, vestiture mostly abraded.

Elytra about as in *hirtus* except strial punctures smaller, interstriae slightly wider than striae, interstrial tubercles on disc more rounded, those on odd-numbered declivital interstriae larger (those on 1 fine, extend to near apex, on 2 five extend to middle, on 3 two at base of declivity, on 7 three on basal third, on 8 four at base, on 9 strongly, acutely elevated, coarsely serrate, about nine serrations). Vestiture of rows of rather coarse, interstrial bristles, short on basal half, longest setae near declivity about as long as distance between rows, absent on even-numbered declivital interstriae.

Type Locality.— Universidad de los Andes Campus, Merida, Merida, Venezuela.

Type Material.— The male holotype was taken at the type locality on 11-IX-1969, 1700 m, No. 5, from *Ficus* bole, by me.

The holotype is in my collection.

Pityophthorus discretus, n. sp.

This species is distinguished from *perotei* Blackman by the larger average size, by the reticulate pronotum which lacks tubercles on the disc, by the more coarsely punctured frons, and by the steeper, more broadly sulcate declivity.

Female.— Length 2.0 mm (paratypes 1.6-2.2 mm), 2.9 times as long as wide.

Frons planoconvex as in *perotei* except more coarsely punctured, vestiture shorter (about two-thirds as long).

Pronotum about as in *perotei* except posterior areas rather strongly reticulate, punctures moderately coarse, deep (tubercles absent).

Elytra about as in *perotei* except disc less shining, almost subreticulate in some specimens; declivity slightly steeper, sulcus slightly deeper and wider.

Male.— Similar to female except frontal vestiture shorter and apparently less abundant.

Type Locality.— Three miles or 5 km W El Salto, Durango, Mexico.

Type Material.— The female holotype, male allotype, and one paratype were taken at the type locality on 7-VI-1965, 2500 m, No. 33, *Pinus ayacahuite*, by me. Other paratypes taken in Mexico by me include: 2 at 29 km or 18 miles W Quiroga, Michoacan, 11-VI-1965, 2300 m, No. 70, *Pinus;* 1 at 9 km or 6 miles E Volcan Paricutin, Jalisco, 19-VI-1965, 2500 m, No. 89, *Pinus;* 1 at 25 km or 14 miles W Texmelucan, Puebla, 14-VII-1953, 2800 m, *Pinus.*

The holotype, allotype, and paratypes are in my collection.

BIOMASS OF FIFTY CONIFER FORESTS AND NUTRIENT EXPORTS ASSOCIATED WITH THEIR HARVEST[1]

T. Weaver[2] and F. Forcella[2]

Abstract.— Biomasses of climax Rocky Mountain forests studied ranged from less than 50 to more than 300 tons/ha. Total biomass was approximately 1.5 times the biomass of normally merchantable boles. When compared with conventional bole harvest, the nutrient exports associated with harvest of all aboveground parts in these stands would apparently be at least three times higher for nitrogen, six times higher for phosphorus, four times higher for potassium, and three times higher for calcium.

The volume or biomass of a tree can be predicted from its diameter or from its diameter and height. Foresters routinely estimate the volume of logs using these dimensions and tables calculated on the assumption that tree trunks are truncated cones or parabolas (Forbes and Meyer 1961). Weights can then be estimated by multiplying their volumes by the density of the wood. In most organisms the size of one organ system is directly related to the size of other organ systems (allometry, Sinnott 1960), so one can predict the volumes or weights of whole organisms from simple measurements. This has been demonstrated for a wide variety of trees including those of the conifer genera *Abies*, *Pinus*, and *Pseudotsuga* (Ovington 1957, Ovington and Madgwick 1959, Kimura 1963, Baskerville 1965, Whittaker and Woodwell 1968, Moir 1972, Odegard 1974, Whittaker et al. 1974, and Long and Turner 1975).

This paper presents a single equation which predicts total aboveground biomass of a tree, from its diameter, for any of the seven most common tree species of the northern Rocky Mountains. A comparison of this equation with others reported in the literature emphasizes the similarity of diameter biomass relationships among conifers in general. Various shrubs may also have similar size-weight relationships (Weaver 1977). An equation predicting weight from measures of both height and diameter is similar to published conifer D^2H-weight relationships but less accurate than the diameter-weight relationship. Similar relationships are presented for weights of boles, branches, twigs, and leaves.

The biomass-DBH relationship found was applied to the stand tables of Daubenmire and Daubenmire (1968) to estimate the aboveground arboreal standing crops of fifty forest stands representing the following climax associations: *Pinus ponderosa-Festuca idahoensis*, *P. ponderosa-Symphoricarpos albus*, *P. ponderosa-Physocarpus malvaceus*, *Pseudotsuga menziesii-Symphoricarpos albus*, *P. menziesii-Physocarpus malvaceus*, *P. menziesii-Calamagrostis rubescens*, and *Abies lasiocarpa-Vaccinium scoparium*.

The nutrient content of the boles and of all aboveground parts was estimated so the nutrient export associated with conventional logging and complete tree utilization could be compared.

Methods

Thirty-nine trees of six coniferous species and one broadleaf species were felled in southcentral Montana. The trees were sectioned into shoot material greater than 10 cm diameter, shoots between one and 10 cm basal diameter, shoots less than 1 cm basal diameter, and leaves. Each class was

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weighed wet. Wet weights were converted to dry weights by multiplying by a conversion factor determined for each component of each tree. The conversion factor was computed as follows: dry weight (60 C to constant weight)/wet weight. The tree species and the numbers of trees per species sampled were *Abies lasiocarpa* (Hook.) Nutt., 7; *Picea engelmannii* (Parry) Engelm., 3; *Pinus contorta* var *latifolia* Engelm., 4; *Pinus ponderosa* Dougl., 6; *Pinus albicaulis* Engelm., 7; *Pseudotsuga menziesii* (Mirb.) Franco., 5; and *Populus tremuloides* Michx., 7. The trees sampled ranged from 4 to 54 cm in diameter at breast height (D at 1.35 m) and from 3 to 20 m in height (H). The trees came from a wide variety of environmental conditions ranging from dry to moist sites and from open to closed stands. A list of the trees and their habitat types, sizes, weights, and ages is available from the authors.

After a preliminary graphical analysis, all data were pooled, and simple and multiple regression analyses were made to determine which models best predicted tree biomass, independent of species. These included linear, curvilinear, and log linear regressions of 12 dependent variables (including weight and logarithms of weights of total shoot and its components) against the independent variables D, D^2, DH, and D^2H.

D^2-biomass relationships were used to estimate the aboveground arboreal biomasses of 50 forest stands for which Daubenmire and Daubenmire (1968) have published stand tables. Since their tables list tree numbers by 10-cm-diameter size classes, tree weights were estimated by two different methods. 1) The weight of all trees in a plot were summed. These weights were estimated by assuming that the diameter of each tree was equal to that of the midpoint of the 10-cm-diameter class in which it was recorded. 2) The weights of all trees in a plot were summed. These weights were estimated by pooling all plot data for a given habitat type on the assumption that it represented a single (abstract) forest; assigning trees in this sample to 2.5-cm-size classes from a balanced distribution of tree size vs tree number (Meyer 1953); and estimating the weights of the trees as if their diameters were equal to the midpoint of the size classes. Regressions through logarithmically transformed data are said to underestimate biomass (Baskerville 1972); we used uncorrected values because graphical analysis suggests that the uncorrected values represent our data better than corrected values do (cf Whittaker et al. 1974).

RESULTS AND CONCLUSIONS

Linear regressions of $\log_{10}D^2$ and $\log_{10}D^2H$ against log weight generally predict biomasses of Rocky Mountain trees well (Table 1 and Fig. 1a). (1) Both independent variables predict total biomass well (r^2 = 0.98 and 0.96, respectively). $\text{Log}_{10}D^2H$ may be the safer predictor if our regressions are used in habitat types where taller trees than ours may be found. (2) $\text{Log}_{10}D^2H$ vs $\log_{10}$ weight is the best predictor for woody material with diameters greater than 1 cm or greater than 10 cm (r^2 = 0.98 and 0.95, respectively). This is likely so because the conic or parabolic models of stem volume are good, weights are strongly correlated with volumes, most of the weight is in the larger classes, and branch volume is both correlated with and overridden by stem volume. (3) $\text{Log}_{10}D^2$ vs $\log_{10}$ weight is the best predictor for leaves and branches with diameters less than 1 cm (r^2 = 0.84 and 0.79, respectively). This may be so because the capacities of current transporting tissues is highly correlated with diameter (cf Shinozaki et al. 1964). A graphical analysis of the leaf weight-diameter relationship suggests that the relatively low r^2 is partly due to between-species differences. (4) A regression of untransformed weights against $D + D^2$ was our best predictor of branch weights (1 to 10 cm, r^2 = 0.97). This curve, not shown, is J-shaped because in small trees the bole is in the branch-size class. (5) Regressions of untransformed variables (D, D^2, DH, D^2H) vs untransformed biomass were not linear, were not used, and are not presented.

Our regressions of $\log_{10}D^2$ or $\log_{10}D^2H$ against $\log_{10}$ weight are remarkably similar to, but not identical with, those determined in other regions (Fig. 1b); predictions of weights from such relationships apparently become poorer as one considers species and environments increasingly different from those for which the relationships were developed. The differences may be due to differences in form factor, wood density, branching patterns, and height-diameter relationships. For example, the tendency of deciduous trees (Monk 1970, Whittaker and Woodwell 1968) to outweigh conifers of similar diameters could be due to the greater wood densities and branchiness of the deciduous trees.

The aboveground arboreal biomasses of 50 stands are summarized in Fig. 2; the val-

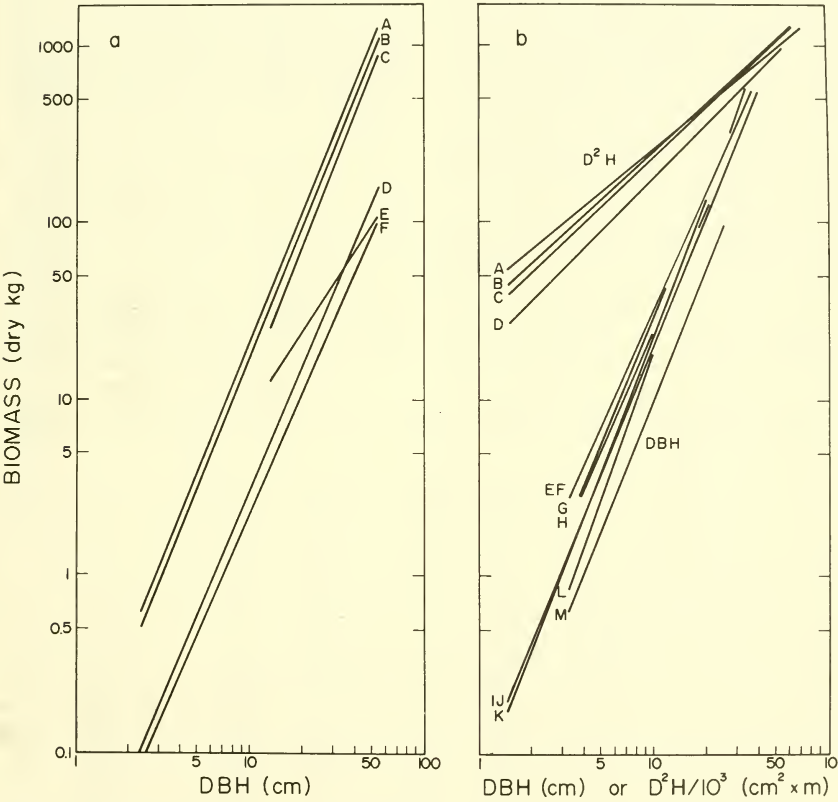

Fig. 1. Biomass-dimension relationships for coniferous species. (A) Diameter-biomass relations for seven species of the northern Rocky Mountains: a = total biomass, b = stem biomass (diameters greater than 1 cm), c = bole biomass (diameters greater than 10 cm), d = twig biomass (diameters less than 1 cm), e = branch biomass (diameters 1-10 cm), and f = leaf biomass. (B) Published DBH-biomass and D²H-biomass relationships: a = *Picea rubens* (Whittaker et al. 1974), b = *Pinus rigida* (Whittaker and Woodwell 1968), c = seven species (Fig. 1a), d = *Pinus contorta* (Odegard 1974), e = *Picea rubens* (Whittaker et al. 1974), f = *Pseudotsuga menziesii* (Long and Turner 1975), g = *Pinus contorta* (Moir 1972), h = *Pinus sylvestris* (Ovington and Madgwick 1959), i = *Pinus rigida* (Whittaker and Woodwell 1968), j = seven species (Fig. 1a), k = *Abies balsamea* (Baskerville 1965), l = *Abies veitchii* (Kimura 1963), and m = *Pinus sylvestris* (Ovington 1957).

ues presented were calculated by assuming that tree diameters were equal to the midpoints of their 10-cm-size classes, i.e., by method 1. One may conclude (1) that total arboreal biomasses of climax conifer stands of the northern Rocky Mountains are generally in the 50-300 tons/ha range and (2) that those of specific forest series or associations generally have a narrower range: Daubenmire's *Pinus ponderosa-Festuca idahoensis* stands had biomasses of 50-150 tons/ha; his *P. ponderosa-Physocarpus malvaceus, Pseudotsuga menziesii-Symphoricarpos albus*, and *Abies lasiocarpa-Vaccinium scoparium* stands had biomasses of 100-250 tons/ha and his *P. menziesii-Physocarpus malvaceus* and *P. menziesii-Calamagrostis rubenscens* stands had biomasses of 100-350 tons/ha. One metric ton/ha = 1000 kg/ha. These estimates of standing crop do not include understory biomasses (perhaps 0.1 to 3 percent or possibly 7 percent of the arboreal biomasses: e.g., Ovington 1962, Whittaker et al. 1974, Tappeiner and John 1973) or belowground biomasses (perhaps 20-30 percent or possibly 7-50 percent of the arboreal biomasses: e.g., Ovington 1962, Rodin and Bazilevich 1965, Whittaker and Woodwell 1968).

Despite the exclusion of understory and underground biomasses, the standing crops reported are larger than most of those reported in the literature (30-70 tons/ha; Rodin and Bazilevich 1965, Art and Marks 1971, Whittaker et al. 1974). Reasons for the large standing crops observed are probably two: Daubenmire selected stands much older than those commonly studied, and he selected the parts of those stands with the biggest trees.

The accuracy of volume and biomass estimates can usually be increased slightly by recording narrower diameter classes (Meyer 1953). To achieve this we pooled the data from all stands occupying a given habitat type on the assumption that it represented multiple stands of one (abstract) forest; determined balanced size distributions (Meyer 1953), allocated trees to 2.5-cm-diameter classes, and estimated their weights by using

TABLE 1. Regression constants and indices of error used in relating sizes and weights of important trees of the northern Rocky Mountains.

		Notes[1]	Total Tree	Wood >1 cm	Wood >10 cm	Wood 1-10 cm	Wood <1 cm	Leaves
D^2	a	2	-1.05	-1.18	-1.40	0.60	-1.87	-1.91
	b	2	1.19	1.21	1.25	0.75	1.16	1.13
	r^2	5	0.98	0.97	0.89	0.81	0.79	0.84
	E	6	1.26	1.34	1.47	1.60	2.23	1.91
D^2H	a	3	1.35	-1.53	-1.84	-0.73	-1.99	-2.08
	b	3	0.93	0.96	1.01	0.57	0.86	0.84
	r^2	5	0.96	0.98	0.95	0.76	0.69	0.77
	E	6	1.36	1.27	1.30	1.72	2.64	2.19
$D+D^2$	a	4	-4.51	+0.08	-29.36	+29.37	-3.02	+1.16
	b	4	-3.32	-2.96	+0.71	-3.69	-0.57	+0.39
	c	4	+0.85	+0.71	+0.49	+0.21	+0.15	+0.06
	r^2	5	0.96	0.96	0.94	0.97	0.63	0.56
	e	6	0.29	0.38	0.25	1.14	0.28	1.00

[1] Identification of symbols to the left.

[2] $\text{Log}_{10}\text{WT} = a + b \log_{10} D^2$ with weight in kg and diameter in cm.

$\text{Log}_{10}\text{WT} = a + b \log_{10} D^2H$ with weight in kg, diameter in cm, and height in m.

$\text{WT} = a + b D + c D^2$ with weight in kg and diameter in cm.

r is the correlation coefficient, r^2 is the fraction of the variation explained by the regression.

E is the antilog of the standard error of a logarithmic regression; expected errors lie between the predicted value x E and the predicted value/E. An estimate of relative error (e) is the standard error of a linear regression divided by the average weight (y) used (Whittaker and Woodwell 1968).

the midpoints of those classes as diameters (method 2). Forest weights estimated by method 2 ranged from 80 to 98 percent of the mean of stand weights determined with 10-cm-diameter classes (i.e., by method 1). They were: *Pinus ponderosa-Festuca idahoensis* 75 tons/ha, 80 percent; *P. ponderosa-Symphoricarpos albus* 155 tons/ha, 82 percent; *P. ponderosa-Physocarpos malvaceus* 140 tons/ha, 98 percent; *Pseudotsuga menziesii-Symphoricarpos albus* 180 tons/ha, 98 percent, *P. menziesii-Calamagrostis rubescens* 336 tons/ha, 91 percent; and *Abies lasiocarpa-Vaccinium scoparium* 178 tons/ha, 93 percent.

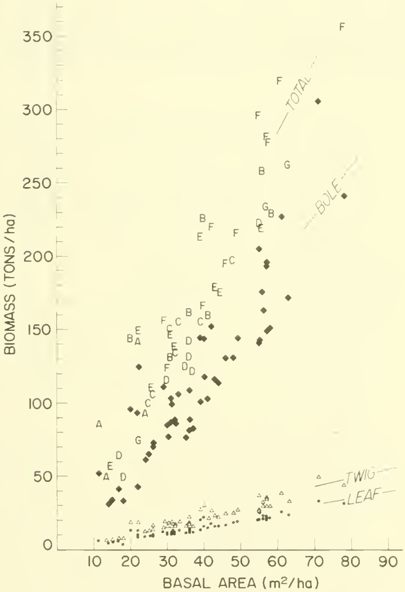

Fig. 2. Aboveground arboreal standing crops of 50 forest stands representing 7 habitat types: *Pinus ponderosa-Festuca idahoensis* (A), *P. ponderosa-Symphoricarpos alba* (B), *P. ponderosa-Physocarpus malvaceus* (C), *Pseudotsuga menziesii-Symphoricarpos alba* (D), *P. menziesii-Physocarpus malvaceus* (E), *P. menziesii-Calamatrostis rubescens* (F), and *Abies lasiocarpa-Vaccinium scoparium* (G). Calculations include all trees with DBH's greater than 5 cm; basal areas of stands 66, 101, 149, 173, 174, and 179 were recalculated from stand table data.

Biomasses in the leaf, twig, branch, and bole compartments are very nearly (SE ± 1 percent) 9 percent, 13 percent, 13 percent, and 66 percent of the arboreal biomass in the mature forests studied. Total harvest in most Rocky Mountain forests should therefore equal approximately 1.5 times the normal (10 cm +) stem harvest (Fig. 2). Whittaker et al. (1974) give similar values. This is a consequence of both the allometric equations used and of the size class distributions observed in the stands studied.

Mineral nutrient export associated with total harvest is greater than 1.5 times that associated with normal bole harvest because needles and bark (which comprise a larger fraction of twigs and branches than of boles) are relatively rich in mineral elements. Table 2 summarizes published values for nitrogen, phosphorus, potassium, and calcium contents for needles, twigs, branches, and boles.

One can estimate the amount of a nutrient element exported from a harvested stand by adding up nutrient export associated with each component exported (Table 2). The nutrient export associated with harvest of any component equals the total export x the proportion (percent) of the total due to the component considered (e.g., needles or bole) x the nutrient content of that component. Since needles, twigs, branches, and boles comprise relatively constant proportions of total aboveground arboreal biomass (9, 13, 13, and 66 percent, respectively), we may conclude that nutrient export associated with total harvest—as opposed to bole harvest alone—is three to six times greater for nitrogen, six to nine times greater for phosphorus, four times greater for potassium, and three times greater for calcium. Thus, total harvest of a Rocky Mountain conifer stand with a relatively low aboveground arboreal biomass of 100 tons/ha might remove 160-460 kg/ha of nitrogen, 20-40 kg/ha of phosphorus, 80-180 kg/ha of potassium, and 120-500 kg/ha of calcium. Bole harvest alone would remove only 25-160 kg/ha of nitrogen, 2-6 kg/ha of phosphorus, 20-40 kg/ha of potassium, and 40-200 kg/ha of calcium. Exports from for-

TABLE 2. Typical nutrient contents of conifers.[1,2]

		Nitrogen		Phosphorus		Potassium		Calcium	
		%	kg/ 100t	%	kg/ 100t	%	kg/ 100t	%	kg/ 100t
Needles	max	1.34	121	0.22	20	0.78	70	1.05	95
	min	0.84	76	0.08	7	0.28	25	0.15	14
Twigs	max	0.60	78	0.07	9	0.30	39	1.10	143
	min	0.31	40	0.05	7	0.14	18	0.27	35
Branches	max	0.77	100	0.06	8	0.25	32	0.54	70
	min	0.15	20	0.02	3	0.12	16	0.28	36
Bole	max	0.24	158	0.01	7	0.06	40	0.30	198
	min	0.04	26	0.00	2	0.03	20	0.06	40
Total	max		457		43		181		506
	min		162		18		79		125

[1] Percentage compositions reported are the highest and lowest values reported for a variety of conifers (*Larix, Picea, Pinus,* and *Pseudotsuga*) in papers by Odegard (1974), Overton et al. (1974), Stark (1973), and Rodin and Bazilevich (1965).

[2] Kg/100t contents refer to 100 tons of aboveground standing crop. They were calculated by multiplying 100 tons of standing crop x the approximate percentage of the standing crop contributed by the organ (9 percent needles, 13 percent twigs, 13 percent branches, and 66 percent boles) x the percentage of the organ contributed by the nutrient considered (N, P, K, or Ca).

est twice to three times as productive would be twice to three times as great.

One wonders whether the forest product value of 'slash' will exceed its fertilizer value. If inputs from nitrogen fixation processes or from decomposition of rocky substrates are small, the fertilizer value of branch material with diameters less than 10 cm might exceed its forest product value.

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THE ALGAL FLORA OF THE CAMPUS OF BRIGHAM YOUNG UNIVERSITY, PROVO, UTAH

Cheng Mou-Sheng[1] and Samuel R. Rushforth[1]

Abstract.— The algal flora of the Brigham Young University campus is more diverse than previously thought. Sixty-eight genera containing 160 species of Chlorophyta, Euglenophyta, Chrysophyta, and Cyanophyta were collected and identified. The greatest number of species was obtained from a small pond in the arboretum, with progressively fewer species obtained in the irrigation canal partly surrounding the campus and in specialized habitats in the greenhouses.

Taxonomic and ecological studies of algae in the Intermountain West and Utah in particular have been rare. The earliest papers on Utah algae concerned the flora of the Great Salt Lake (Rothpletz 1892, Talmage 1900, Daines 1917). This unusual habitat has continued to be of interest to the present time and is currently under study by several biologists and water quality specialists.

Other early papers on Utah algae were those of Norrington (1925) on the algae of the lakes and streams of the Uinta and Wasatch Mountains of Utah; Harrison (1926) on the algae of Washington County, Utah; Tanner (1930, 1931) on the algae of Utah Lake; Snow (1932) on the algae of Utah Lake; Kirkpatrick (1934) on the biology of the Great Salt Lake; and Patrick (1936) on the diatoms in core samples from the edge of the Great Salt Lake.

The algal flora found on the Brigham Young University campus has been under observation for several years, particularly for teaching purposes. However, nothing has been written concerning this flora until recently. The most important contribution to a knowledge of this flora was made by the senior author of the present paper in a study during 1971-1972 for the research requirement for the Master of Science degree (Mou-Sheng 1973). The junior author has continued to collect algae from the campus since that time.

Methods

Several collecting stations were established at selected sites on the Brigham Young University campus. Sites were established in the arboretum pond, the irrigation canal transversing the campus, and in the Department of Botany and Range Science greenhouses. Phytoplankton, attached algae, and algae in the sediments were all sampled. In addition several physical and chemical parameters were measured at the aquatic sites in order to provide an overall picture of the environment.

Algae were returned to the laboratory, subsampled, and examined immediately for nondiatom algae. These were studied using a Zeiss RA microscope with Nomarski interference phase accessories. Algae were identified using standard reference texts.

Following study of the nondiatoms, permanent diatom slides were prepared by standard boiling nitric acid tenchiques. Diatoms were mounted in pleurax diatom mountant. These slides are in the Brigham Young University diatom collection. Diatoms were examined with the same equipment cited above and identified by us, using standard reference texts.

Results

Sixty-eight genera and 160 species of algae have been identified and described from the campus. This flora consists of 27 genera containing 36 species of Chlorophyta, 2 genera containing 2 species of Euglenophyta, 32 genera containing 106 species of Bacillariophyceae, 1 genus containing 2 species of Chrysophyta excluding diatoms, and 6 genera containing 14 species of Cyanophyta.

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The Brigham Young University arboretum pond affords an excellent habitat for the growth of algae. This pond contains high levels of dissolved silica (27-81 PPM), bicarbonates, carbon dioxide (8-68 PPM) and oxygen (5-12 PPM) which support a high population of diatoms throughout the winter and spring and Chlorophyta (especially *Spirogyra dubia* Kutzing, S. *jugalis* [Dan.] Kutzing, S. *neglecta* [Hass.] Kutzing and S. *porticalis* [Muell.] Cleve) through the late spring and summer.

The diatom flora of the arboretum pond is dominated by *Melosira varians* Agardh, *Synedra parasitica* var. *subconstricta* (Grun.) Hust., S. *ulna* (Nitz.) Ehr., S. *ulna* var. *subaequalis* (Grun.) v. Heur., *Cocconeis pediculus* Ehr., *C. placentula* var. *lineata* (Ehr.) v. Heur., *Anomoconeis sphaerophora* (Kutz.) Pfitz., *Cymbella cistula* (Hemprich) Grun., *Nitzschia linearis* W. Sm., *N. sigmoidea* (Ehr.) W. Sm., and *Cymatopleura solea* (Breb.) W. Sm.

Several species of diatoms, especially of *Navicula*, *Cymbella*, and *Nitzschia* have been found only in this pond on campus. These include *Navicula cuspidata* (Kutz.) Kutz., *N. odiosa* Wallace, *N. placentula* var. *rostrata* Mayer, *N. pupula* Kutz., *N. pygmaea* Kutz., *Cymbella heteropleura* (Ehr.) Kutz., *C. mexicana* (Ehr.) Schmidt., *C. prostrata* (Berk.) Cl., *C. tumida* (Breb.) v. Heur., *C. tumidula* Grun., *C. turgida* Greg., *Nitzschia hungarica* Grun., *N. sigma* (Kutz.) W. Sm., and *N. tryblionella* Hantz. Other species restricted to this locality were *Melosira distans* (Ehr.) Kutz., *Fragilaria brevistriata* var. *inflata* (Pant.) Hust., *Synedra capitata* Ehr., *Eunotia curvata* (Kutz.) Lagerst, *Caloneis ventricosa* (Ehr.) Meist., *Neidium iridis* (Ehr.) Cl., *Gomphonema acuminatum* Ehr., *Epithemia turgida* (Ehr.) Kutz., *E. turgida* var. *granulata* (Ehr.) Grun., and *Rhopalodia gibba* (Ehr.) O. Mull.

The Brigham Young University botanical greenhouses represent rather specialized environmental conditions. Thus, several parameters such as light, water, and temperature are controlled and demonstrate little fluctuation. The algal flora of the greenhouses is dominated by *Protococcus viridis* Agardh, *Chlorococcum humicola* (Naeg.) Rabenhorst, *Oscillatoria sancta* (Kutz.) Gomont, *Amphora normani* Rabh., and *Hantzschia amphioxys* (Ehr.) Grun.

Several species of algae have been colected on campus only from the greenhouses. These include *Lyngbya aestuarii* (Mertens) Liebmann, *L. martensiana* Meneghini, *Oscillatoria angustissima* West and West, *O. animalis* Agardh, *O. cruenta* Grun., *O. limosa* (Roth) Agardh, *O. sancta* (Kutz.) Gomont, *O. tenuis* Agardh, *Phormidium inundatum* Kutzing, *Anabaena variabilis* Kutzing, *Tolypothrix penicillata* (Ag.) Thur., *Stichococcus bacillaris* Naegeli, S. *scopulinus* Hazen, S. *subtilis* (Kutz.) Klercker, and *Chlorella vulgaris* Beyerinck.

Sixteen genera containing 33 species of diatoms have been collected from the soil in

Table 1. Number of species of algae on the Brigham Young University campus by algal division and collection locality.

Algal Division	Collection Locality		
	Arboretum Pond	Campus Stream	Greenhouses
Chlorophyta	10	5	8
Euglenophyta	1	0	0
Chrysophyta	84	80	33
Cyanophyta	1	2	13
TOTAL	96	87	54

the campus greenhouses. *Hantzschia amphioxys* (Ehr.) Grun. and *Amphora normani* Rabh. are the most common soil diatoms. *Achnanthes lanceolata* (Breb.) Grun., *Navicula tripunctata* (Mull.) Bory, *Hantzschia amphioxys* var. *capitata* Mull., and *Nitzschia palea* (Kutz.) W. Sm. are also quite common. *Pinnularia gentilis* (Donk.) Cl. is the only diatom restricted to the soil.

The water in the irrigation canal that crosses the Brigham Young University campus generally has higher levels of nitrates, phosphates, dissolved oxygen, alkalinity, and carbon dioxide than the arboretum pond. It contains near the same number of species of algae but has a lower standing crop due to the paucity of filamentous Chlorophyta.

The flora of this stream is dominated by *Stephanodiscus niagare* Ehr., *Diatoma vulgare* Bory, *D. tenue* var. *elongatum* Lyngb., *Cocconeis pediculus* Ehr., *C. placentula* var. *euglypta* (Ehr.) Cl., *Navicula tripunctata* (Mull.) Bory, *Gomphonema olivaceum* (Lynbye) Kutz., and *Nitzschia sigmoidea* (Ehr.) W. Sm.

Species found only in this stream include *Chaetophora incrassata* (Huds.) Hazen, *Diatoma hiemale* var. *mesodon* (Ehr.) Grun., *Gomphonema acuminatum* var. *coronatum* (Ehr.) W. Sm., *G. angustata* var. *sarcophagus* (Greg.) Grun., *Hannaea arcus* var. *amphioxys* (Rabh.) Patr., *Navicula capitata* Ehr., *Navicula laevissima* Kutz., *N. mutica* Kutz., *Neidium affine* (Ehr.) Pfitz., *Palmella mucosa* Kutz., and *Synedra ulna* var. *constricta* Ostr.

The following list contains those algae collected on the Brigham Young University campus.

CHLOROPHYTA
- Chlorophyceae
  - Chlorococcales
    - Chlorococcaceae
      - *Characium ambiguum* Hermann
      - *Chlorococcum humicola* (Naeg.) Rabenhorst
    - Palmellaceae
      - *Palmella mucosa* Kutzing
      - *Sphaerocystis schroeteri* Chodat
    - Oocystaceae
      - *Chlorella vulgaris* Beyerinck
    - Scendesmaceae
      - *Scenedesmus denticulatus* Lagerheim
      - *S. quadricauda* var. *quadrispina* (Chod.) G. M. Smith
    - Hydrodictyaceae
      - *Pediastrum boryanum* (Turp.) Meneghini
      - *P. tetras* (Ehreb.) Ralfs
  - Ulotrichales
    - Protococcaceae
      - *Protococcus viridis* C. A. Agardh
    - Ulotrichaceae
      - *Stichococcus bacillaris* Naegeli
      - *S. scopulinus* Hazen
      - *S. subtilis* (Kutz.) Klercker
      - *Ulothrix zonata* (Weber & Mohr) Kutzing
  - Chaetophorales
    - Aphanochaetaceae
      - *Aphanochaete repens* A. Braun
    - Chaetophoraceae
      - *Chaetophora incrassata* (Huds.) Hazen
      - *Stigeoclonium lubricum* (Dillw.) Kutzing
  - Oedogoniales
    - Oedogoniaceae
      - *Oedogonium* sp.
  - Cladophorales
    - Cladophoraceae
      - *Cladophora glomerata* (L.) Kutzing
  - Zygnematales
    - Zygnemataceae
      - *Mougeotia genuflexa* (Dillw.) C. A. Agardh
      - *Spirogyra dubia* Kutzing
      - *S. jugalis* (Fl. Dan.) Kutzing
      - *S. neglecta* (Hass.) Kutzing
      - *S. porticalis* (Muell.) Cleve
      - *Zygnema insigne* (Hass.) Kutzing
    - Desmidiaceae

TABLE 2. Number of species of algae on the Brigham Young University campus restricted to selected collection localities.

Algal Division	Collection Locality		
	Arboretum Pond	Campus Stream	Greenhouses
Chlorophyta	8	4	8
Euglenophyta	1	0	0
Chrysophyta	22	18	3
Cyanophyta	0	0	12
TOTAL	31	22	23

Closterium lanceolatum Kutzing
C. moniliferum (Bory) Ehrenberg
Cosmarium botrytis Meneghini
C. perforatum Lund.
Penium navicula Breb.

EUGLENOPHYTA
Euglenophyceae
Euglenales
Euglenaceae
Euglena acus Ehrenberg
Phacus acuminata Stokes

CHRYSOPHYTA
Xanthophyceae
Vaucheriales
Vaucheriaceae
Vaucheria geminata (Vaucher) DeCandolle
V. sessilis (Vaucher) DeCandolle
Bacillariophyceae
Centrales
Coscinodiscaceae
Melosira distans (Ehr.) Kutz.
M. granulata (Ehr.) Ralfs
M. italica (Ehr.) Kutz.
M. varians C. A. Ag.
Cyclotella bodanica Eulenst.
C. meneghiniana Kutz.
Stephanodiscus niagare Ehr.
Pennales
Fragilariaceae
Asterionella formosa Hassall
Hannaea arcus var. *amphioxys* (Rabh.) Patr.
Diatoma anceps (Ehr.) Kirch.
D. hiemale var. *mesodon* (Ehr.) Grun.
D. tenue var. *elongatum* Lyngb.
D. vulgare Bory
Fragilaria brevistriata var. *inflata* (Pant.) Hust.
F. capucina var. *mesolepta* Rabh.
F. construens var. *venter* (Ehr.) Grun.
F. crotonensis Kitton
F. leptostauron (Ehr.) Hust.
F. vaucheria (Kutz.) Peters.
Meridion circulare var. *constrictum* (Ralf.) v. Heur.
Synedra acus Kutz.
S. capitata Ehr.
S. fasciculata (Ag.) Kutz.
S. parasitica (W. Sm.) Hust.
S. parasitica var. *subconstricta* (Grun.) Hust.
S. rumpens Kutz.
S. ulna var. *subaequalis* (Grun.) v. Heur.
S. ulna var. *constracta* Ostr.
S. ulna var. *ramesi* (Herib.) Hust.
S. ulna var. *ulna* (Nitz.) Ehr.
Eunotiaceae
Eunotia curvata (Kutz.) Lagerst
Achnanthaceae
Achnanthes lanceolata var. *dubia* Grun.
A. lanceolata var. *lanceolata* (Breb.) Grun.
A. minutissima Kutz.
Cocconeis pediculus Ehr.
C. placentula var. *euglypta* (Ehr.) Cl.
C. placentula var. *lineata* (Ehr.) v. Heur.
Rhiocosphenia curvata (Kutz.) Grun. ex Rabh.
Naviculaceae
Anomoeoneis sphaerophora (Kutz.) Pfitz.
Caloneis ventricosa (Ehr.) Meist.
Diploneis oblongella (Naeg. ex Kutz.) Ross
Frustulia vulgaris (Thwaites) DeT.
Gyrosigma spencerii (Quek.) Griff. & Henfr.
Navicula capitata Ehr.
N. cryptocephala Kutz.
N. cryptocephala var. *veneta* (Kutz.) Rabh.
N. cuspidata (Kutz.) Kutz.
N. elginensis (Greg.) Ralfs
N. laevissima Kutz.
N. lanceolata (Ag.) Kutz.
N. mutica Kutz.
N. oblonga (Kutz.) Kutz.
N. odiosa Wallace
N. plancentula var. *rostrata* A. Mayer
N. pupula Kutz.
N. pygmaea Kutz.
N. rhynchocephala Kutz.
N. tripunctata (O. F. Mull.) Bory
Neidium affine (Ehr.) Pfitz.
N. binode (Ehr.) Hust.
N. iridis (Ehr.) Cl.
Pinnularia brebissonii (Kutz.) Rabh.
P. gentilis (Donk.) Cl.
P. viridis (Kutz.) Ehr.
Stauroneis smithii Grun.
Gomphonemaceae
Gomphonema acuminatum Ehr.
G. acuminatum var. *coronatum* (Ehr.) W. Sm.
G. angustata var. *sarcophagus* (Greg.) Grun.
G. constrictum Ehr.
G. intricatum Kutz.
G. olivaceum (Lyngbye) Kutz.
G. olivaceum var. *calcarea* Cl.
G. parvulum (Kutz.) Grun.
G. parvulum var. *micropus* (Kutz.) Cl.
Cymbellaceae
Amphora ovalis Kutz.
A. normani Rabh.
Cymbella affinis Kutz.
C. aspera (Ehr.) Cl.
C. cistula (Hemprich) Grun.
C. ehrenbergii Kutz.
C. heteropleura (Ehr.) Kutz.
C. mexicana (Ehr.) A. Schmidt
C. prostrata (Berk.) Cl.
C. tumida (Breb.) v. Heur.
C. tumidula Grun.
C. turgida Greg.
C. ventricosa Kutz.
Epithemiaceae
Epithemia sorex Kutz.
E. turgida (Ehr.) Kutz.
E. turgida var. *granulata* (Ehr.) Grun.
Rhopalodia gibba (Ehr.) O. Mull.
Nitzschiaceae
Hantzschia amphioxys (Ehr.) Grun.
H. amphioxys var. *capitata* Mull.
Nitzschia amphibia Grun.
N. dissipata (Kutz.) Grun.

- *N. fonticola* Grun.
- *N. hungarica* Grun.
- *N. linearis* W. Sm.
- *N. palea* (Kutz.) W. Sm.
- *N. sigma* (Kutz.) W. Sm.
- *N. sigmoidea* (Ehr.) W. Sm.
- *N. tryblionella* Hantz.
- Surirellaceae
  - *Cymatopleura solea* (Breb.) W. Sm.
  - *Surirella angustata* Kutz.
  - *S. ovalis* Breb.
  - *S. ovata* var. *pinnata* W. Sm.
  - *S. robusta* Ehr.

- CYANOPHYTA
  - Myxophyceae
    - Chroococcales
      - Chroococcaceae
        - *Chroococcus rufescens* (Kutz.) Naegeli
    - Oscillatoriales
      - Oscillatoriaceae
        - *Lyngbya aestuarii* (Mertens) Liebmann
        - *L. martensiana* Meneghini
        - *Oscillatoria amphibia* C. A. Agardh
        - *O. angustissima* West & West
        - *O. animalis* C. A. Agardh
        - *O. cruenta* Grun.
        - *O. limosa* (Roth) C. A. Agardh
        - *O. princeps* Vaucher
        - *O. sancta* (Kutz.) Gomont
        - *O. tenuis* C. A. Agardh
        - *Phormidium inundatum* Kutzing
    - Nostocales
      - Nostocaceae
        - *Anabaena variabilis* Kutzing
      - Scytonemataceae
        - *Tolypothrix penicillata* (Ag.) Thur.

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OCCURRENCE OF TICKS ON MULE DEER IN CENTRAL UTAH

Jordan C. Pederson[1]

Abstract.— Two species of ticks were collected from mule deer and identified as *Dermacentor albipictus* (Packard) and *Ixodes* sp. The rate of occurrence of these ticks was found to be 99.6 percent and 0.4 percent, respectively. The infestation rate increased from 18.2 percent in January, to 87.5 percent in February, to 100.0 percent in March.

From January through March 1976, a mule deer (*Odocoileus hemionus Rafinesque*) trapping operation was conducted by Utah State University, the Cooperative Wildlife Research Unit, and the Utah State Division of Wildlife Resources. The principal emphasis of this study was the gathering of deer reproduction data. Deer were live-trapped, weighed, and ear-tagged, and a laparotomy was performed on all females. Additionally, a blood sample was taken from each animal. These deer were also checked for external parasites. This paper reports the occurrence of ticks on mule deer in central Utah based on this study. Appreciation is extended to Dr. C. Selby Herrin for his help in the identification of the parasites collected. The help of Paul Tervort, Dick Worthen, and Phil Zwank is gratefully acknowledged. Thanks are also extended to Dr. S. L. Welsh and R. Drobnick for their critical review of this manuscript.

Harris (1945) reported associations of *Dermacentor albipictus* (Packard) on mule deer in a South Dakota study dealing with malnutrition in deer. He states, "In a few cases the factors contributing to the death (deer) were predators or minor infestation of internal and external parasites, such as nose bot (*Cephenomyia*) and winter tick (*Dermacentor albipictus*)." Edmunds (1951) gives an account of *D. albipictus* on deer near Logan, Utah, collected by Clamaine in 1942. Beck (1955) regards *D. albipictus* as localized in distribution and a potential vector of Rocky Mountain spotted fever. Richens (1967) found this parasite on mule deer in Daggett County, Utah, where the proportion of deer infested with this tick rose from 37 percent in January to 92 percent in March of 1960. This parasite was also reported on deer in Garfield, Grand, San Juan, and Wayne counties in Utah by Pederson (1970); deer on the La Sal and Henry mountains were shown to have an infestation rate of 55 and 75 percent, respectively, or a combined occurrence of 63 percent.

Members of the genus *Ixodes* have not previously been reported on deer in Utah, although they are found as juveniles during winter months in association with small mammals (Edmunds 1951).

Methods and Procedures

Live trapped deer were systematically examined for external parasites. Those found were removed and placed in isopropyl alcohol (70 percent). The site of occurrence or attachment was noted. Data recorded for the host animals included sex, age, ear tag number, weight, and an estimate of general body condition. Deer killed by motor vehicles were examined as part of this study. An effort was made to collect a representative sample of ectoparasites at each site of attachment on the deer. All other ticks were removed to obtain data on reinfestation rates on live-trapped deer.

All deer examined during 1976 were from Utah County, specifically the areas of Long Hollow, Knoll Hollow, Lasson Draw, and Spanish Fork Canyon.

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RESULTS AND DISCUSSION

Two species of ticks were collected and identified, *Dermacentor albipictus* and *Ixodes* sp. The rate of occurrence of these ticks on mule deer was 99.6 percent and 0.4 percent, respectively. *Dermacentor albipictus* specimens collected were identified as 35.6 and 57.3 percent adult males and females, respectively; 6.7 percent nymphs, and 0.4 percent larvae (Table 1). Adult females made up the largest percentage of the population for January, with a 66.6 percent occurrence rate. Adult males were highest in the population in February at 39.8 percent and lowest in March at 27.1 percent. Nymphs were first collected during February and were highest during March (14.4 percent), with an average occurrence of 6.7 percent during this study (Table 1). Their occurrence rate varied from zero in January to 14.4 percent in March.

During this study two female specimens of *Ixodes* sp. were collected, one in January and one in February. Both were collected in Long Hollow from two female mule deer older than five years.

The number of deer infected by ticks varied by age class and month. The highest rate of infestation was in the fawn age class, where it averaged 95.1 percent during this study (Table 2). The deer of 1¾ and 2¾ age classes were very similar in their monthly and total infestation rates (Table 2). Mature deer (three years and older) had an infestation rate exceeded only by fawns. They were the highest infested age class for February, with a 87.5 percent infestation rate (Fig. 2). All age classes had a 100 percent infestation during March. The infestation rate for all age classes for the duration of the study was 84 percent.

Data gathered on the point of attachment of ticks on each deer showed that three specific points of attachment accounted for 94.6 percent of the ticks. The largest number of *D. albipictus* were attached around the anus (49.7 percent), the ears were the next highest (39.7 percent), the areas of the flank and udder accounted for 5.3 percent, and the remaining 5.3 percent were attached to other parts of the body. Ticks were usually found on the body areas of short and very sparse hair growth.

Five of the deer captured during the study were retaken and reexamined during subsequent trapping periods. Three were fawns (1 male, 2 female) and two were mature females. A female fawn trapped in Long Hollow on 24 January 1976 was examined and found to be free of external parasites. When this deer was retrapped on 23 February 1976 three male and eight female were found attached near the anus. She had lost 1.8 kg, a 5 percent loss in body weight, possibly due in part to the presence of ticks. The remaining four deer all had *D. albipictus* present on their ears and near the anus when first captured. All ticks were removed. When recaptured, all had *D. albipictus* present on their ears and near the anus. One of these, a female fawn retrapped 16 days after initial capture, had lost 1.4 kg. This is also a 5 percent loss in body weight. The other three deer, one male fawn and two mature does, expe-

TABLE 1. Occurrence on mule deer of *Dermacentor albipictus* by developmental stage, sex and month. The percentage of ticks comprising each sex or life stage for each month appears in parentheses following the number found.

Month	Adult Male	(%)	Adult Female	(%)	Nymph	(%)	Larva	(%)	Total
January	2	(33.4)	4	(66.6)	0	(0.0)	0	(0.0)	6
February	155	(39.8)	220	(56.5)	12	(3.1)	1	(0.3)	389
March	53	(27.1)	114	(58.5)	28	(14.4)	0	(0.0)	195
Total	210	(35.6)	338	(57.3)	40	(6.7)	1	(0.4)	590

TABLE 2. Infestation rate of *Dermacentor albipictus* on mule deer by month and age class.

Month	Deer Age														
	Fawn			1¾ Years			2¾ Years			3 Years and Over			Summary		
	Number examined	Number infected	Percent infected	Number examined	Number infected	Percent infected	Number examined	Number infected	Percent infected	Number examined	Number infected	Percent infected	Number examined	Number infected	Percent infected
January	2	1	50.0	2	0	0.0	1	0	0.0	6	1	16.7	11	2	18.2
February	30	29	96.6	8	5	62.5	8	5	62.5	38	34	89.4	80	70	87.5
March	9	9	100.0	2	2	100.0	1	1	100.0	16	16	100.0	28	28	100.0
Total	41	39	95.1	12	7	58.3	10	6	60.0	51		85.0	119	100	84.0

rienced no loss of body weight. During this study no deer mortality could be attributed to infestation of ticks.

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POPULATION DYNAMICS OF THE FERRUGINOUS HAWK DURING A PREY DECLINE

Neil D. Woffinden[1] and Joseph R. Murphy[2]

ABSTRACT.— A nesting population of Ferruginous Hawks (*Buteo regalis*) at the eastern edge of the Great Basin in west-central Utah was studied for three nesting seasons, 1972-1974, during which time a significant decline in jackrabbit numbers occurred. The total number of hawks and nesting pairs varied throughout the study. In 1972, 16 pairs occupied territories and only 1 pair failed to nest. By 1974, however, only 5 pairs and 2 single birds occupied territories. The number of young fledged ranged from 31 in 1972 to 3 in 1974. The nesting phenology of the Ferruginous Hawk and the reproductive period of black-tailed jackrabbits are clearly correlated. Of the jackrabbit remains collected from hawk nests, 90 percent were from rabbits younger than 13 weeks. The decline in hawk numbers is thought to be directly correlated with a drop in the jackrabbit population.

How to get something to eat and how to keep from being eaten are among the most fundamental requirements of life. These factors have a tremendous impact on the structure, abundance, and community integration of an organism (Huffaker 1970: 327).

Much has been written about predation; yet many questions remain unanswered. Brown (1970: 247) suggested that seasons and breeding cycles of certain raptor species have never been properly correlated with behavior and abundance of their prey. In this study we sought to determine the effect of prey density on the nesting success of the Ferruginous Hawk (*Buteo regalis*) and to investigate the timing of predator and prey reproductive cycles and establish, if possible, a correlation between these two events. Finally, since little was known at the time of this study about the Ferruginous Hawk, we felt that any general knowledge of this species gained in the study would be of value.

Funding was provided in part by the National Audubon Society and the Department of Zoology, Brigham Young University, Provo, Utah. Gerald Richards and Reed Ferris aided in field work, and D. M. Allred and C. M. White gave valuable criticism of the manuscript.

METHODS AND PROCEDURES

The study was conducted from June 1972 through October 1974 within an area of approximately 932 km^2, involving portions of Utah and Tooele counties in northcentral Utah. Most of the field work was carried out during the nesting season, but we made monthly observations from October 1973 through October 1974. During the periods of intensive study, several visits were made to the study area each week (Fig. 1).

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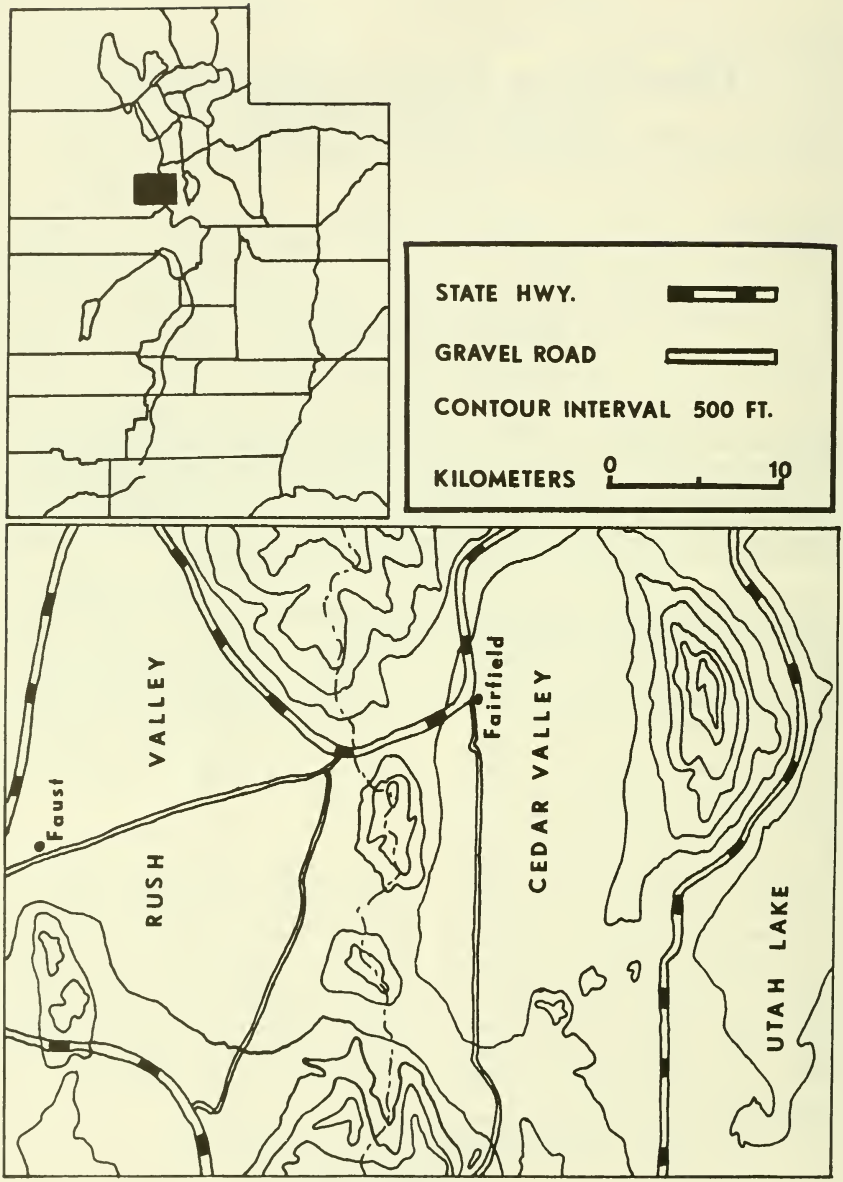
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GRAVEL ROAD
CONTOUR INTERVAL 500 FT.
KILOMETERS
0
10
RUSH VALLEY
Faust
Fairfield
CEDAR VALLEY
UTAH LAKE

Fig. 1. Study area location.

A smaller portion of the overall study area (238 km^2) was selected for intensive study. This area coincides approximately with the boundaries of Cedar Valley, one of the eastern valleys of the Great Basin valley-and-range complex.

The intensive study area, henceforth referred to as Cedar Valley, was systematically searched for Ferruginous Hawk nests in 1972 and 1973. Previous studies (Murphy et al. 1969, Smith and Murphy 1973) and banding records were also utilized in nest location and production for 1972 and previous years. An effort was made to locate inactive as well as active nests in both Cedar Valley and the western part of adjoining Rush Valley.

Prey remains and castings were collected regularly from the active nests. Identification of prey items was made by comparison to known specimens. The length of rabbit feet found in and around the nests was recorded and compared with tables in Haskell and Reynolds (1947) to estimate ages and weights.

Black-tailed jackrabbits (*Lepus californicus*) density indices were obtained by use of line transects. Five randomly distributed, square transects .25 km on a side (Gross 1967) were conducted periodically throughout the latter part of the study. The transect leg and direct distance from the observer to the point of flush was recorded for each rabbit flushed. The angle formed by the transect line and a line from the observer to the point where the animal was located was measured to the nearest degree.

Numbers of road-killed jackrabbits observed during regular visits to the study area as well as during winter raptor surveys were recorded. By expressing the number of kilometers traveled per road-killed jackrabbit, an index of abundance was obtained. During the latter part of the study, hind foot lengths were recorded for each road-killed jackrabbit.

Clutch size, fledging rates, and other production figures were determined by regular nest visits throughout the nesting season.

Statistical tests used include student "t" analysis of variance, and chi square tests. The level of significance is 0.05 unless stated differently.

Results

The black-tailed jackrabbit was abundant in the study area during the 1972 nesting season. It was not uncommon, during a visit to the study area, to see as many as 15 jackrabbits flush before the vehicle. Active nests during this season were cluttered with jackrabbit remains. One nest contained remains of at least 24 jackrabbits. Unfortunately, we were unable to obtain objective population densities. Gross et al. (1974), however, gave jackrabbit density indices for a nine-year period (1962-1970) for their northern Utah study area. The indices represented approximately the number of jackrabbits per km^2 (Gross et al. 1974: 27). They recorded in the autumn of 1970 a peak density of 71.4 jackrabbits per km^2. Stoddart (pers. comm. and in Howard 1975) reported a spring 1972 density of 47.1 jackrabbits per km^2 in the same area. This value dropped sharply to 9.7 km^2 in the spring of 1973. We assume that population densities in Cedar Valley were similar to those in northern Utah during the 1972 nesting season.

We also observed a decline in jackrabbit numbers between the 1972 and 1973 nesting seasons. One nest active in 1973 contained no rabbit remains. This nest was in the area of peak 1972 nesting density. An area of 27,225 m^2 near this nest was systematically searched four times for jackrabbits. One rabbit was flushed in each of the first three searches but none on the last search. The three flushes may have represented one individual.

In 1974 five randomly selected transects located throughout the study area were walked to establish jackrabbit densities (Table 1). These transects were similar to those used by Gross et al. (1974). Only one area had a density greater than one (1.0) rabbit/km^2 (Table 1). The number of kilometers per rabbit sighted varied from 0.46 in the area of highest densities to 8.0 in an area where only one jackrabbit was sighted.

In addition to the transects, during the first eight months of 1974 the number of road-killed jackrabbits observed was recorded. Over 19,948 km were traveled during this period and 122 jackrabbits were counted (Table 2), for an average number of 89.7 kilometers traveled per jackrabbit.

In spite of a lack of quantification, we feel that jackrabbit numbers dropped significantly in our study area, as they did in northern Utah, between the 1972 and 1973 nesting seasons. Numbers continued to remain low in 1974. This decline in prey numbers had a significant impact on the Ferruginous Hawk population in Cedar Valley.

The total number of birds and number of nesting pairs varied throughout the study. Table 3 summarizes these data for an eight-year period. In 1972, 16 pairs occupied territories in the intensive study area. There were no single birds present. Only one pair failed to make a nesting attempt. A total of nine pairs occupied nesting territories in 1973; of these, two pairs failed to nest. No single birds were observed. In 1974 five pairs of birds occupied territories; two pairs failed to nest and two single birds were observed occupying territories (Fig. 2).

Table 1. Number of transects, total rabbits observed, and mean density index of jackrabbits for Cedar Valley, 1974.

Location	No. Transects Walked	No. Rabbits Counted	Km/ Rabbit	Density Index Rabbits/ Km^2
Cat Hill	6	7	1.37	0.17
Long Point	10	35	0.46	1.33
Roadtop Hill	5	1	8.0	0.06
Carrol	11	16	1.1	0.32
Quarry	3	0	–	–

Table 2. Number of road-killed jackrabbits, January-August 1974.

Month	No. Roadkills	No. Km Traveled	No. Km per Roadkill
Jan	4	1310.5	327.6
Feb	0	1145.2	–
Mar	5	1163.7	232.7
Apr	4	569.1	142.3
May	8	1664.4	208.1
Jun	33	2002.5	60.7
Jul	46	2355.4	51.2
Aug	22	822.7	37.4
Totals	122	11033.5	90.4

The total population varied from 32 birds present in 1972 to 18 in 1973 and 12 in 1974. Single individuals were observed only in 1974. A marked decline occurred over the three-year study, with the peak population occurring in 1973 (32 birds) and a low in 1974 (12 birds). The average number of birds present (for the study period) was 20.7, with a range of 12-32. The average number of Ferruginous Hawks occupying territories from 1967 to 1970 was 19 (range 18-27). The average number for the study period did not vary significantly from the average for the four-year period 1967-1970.

In 1972 there were 14.85 km^2 per pair of birds in the intensive study area. This value increased to 26.24 km^2 and 34.03 km^2 for 1973 and 1974, respectively. It should be noted, however, that much of the habitat of Cedar Valley is unsuitable for nesting. The previous values are thus misleading because nests were placed on the hills surrounding the valley and no nests were found on the valley floor proper. The relative changes in nesting density during the study, however, would remain the same.

In 1972, 94 percent of the resident pairs nested. This value then dropped to 77.8 percent and 42.9 percent for 1973 and 1974. The average for the three year period was 71.6 percent.

Clutch Size.— Disturbance of Ferruginous Hawks during incubation is a significant cause of nest desertion (Powers et al. 1973, Olendorff 1973), and therefore few nests were visited during incubation. Thus, an accurate clutch size was not recorded for all nests. However, by extrapolating back from the number of young hatched, or in some cases fledged, a minimum clutch size was obtained. Minimum clutch sizes will be given, but it should be kept in mind that the numbers presented probably underestimate the true clutch size.

Minimum clutch size varied from a high of 2.7 in 1972 to 2.1 and 2.4 in 1973 and 1974. The average clutch size for these three years is 2.4. More complete data on clutch size was obtained by Weston (Murphy et al. 1969) and Smith and Murphy (1973).

Mortality.— Nestling mortality was high during the study. Data are not available for the 1972 nesting season, but, based on the number of young fledged from each nest, mortality appeared to be negligible. An average nestling mortality of 49.5 percent was, however, calculated for the 1973 and 1974 nesting seasons. This value is significantly greater than the 13.3 percent average calculated from the 1967-1970 data (Murphy et al. 1969, Smith and Murphy 1973).

In 1973 when the nests were visited regularly during incubation, two of the three nests in the southeastern end of the study area failed. Four chicks were lost in these two nests. One of the two chicks in the third nest disappeared during the first weeks after hatching. This may have been a case of cannibalism, or the bird may have died and was then eaten. The agent responsible for the deaths of the other young birds is not known. The striped skunk *(Mephitis mephitis)* was observed in the area as was the coyote *(Canis latrans)*. A cliff near the nests was apparently used by Great Horned Owls as a roost. They or other raptors in the area could have taken the young. One nest was blown out of a tree during the 1973 nesting season. Thus, three of the six nests (50 percent) were completely destroyed, contributing to a nestling mortality of 42 percent.

High nestling mortality occurred during the 1974 nesting season. Three nests hatched a total of seven young and fledged only three. Each nest fledged one young hawk. One young bird large enough to leave the nest, approximately five weeks old, was found dead beside the nest. Examination suggested that it died of starvation. Earlier, approximately three weeks after hatching, one nestling had disappeared from

Table 3. Ferruginous Hawk territory occupation and nesting attempts, 1967-1974.

Year	No. Pairs	No. Single Birds	No. Territories Occupied	No. Nesting Attempts	Percent Nesting per Occupied Territories	Area per Territory Km^2	Location[5]
1967[1]	13	–	13	13	100	18.34	CV
1968[1]	14	–	14	14	100	17.02	CV
1969[2]	13	1	14	12	85.7	17.02	CV
1970[2]	9	2	11	7	63.6	21.65	CV
1971[3]	5	0	5	5	100	–	CV
1972	16	0	16	15	94	14.85	CV
1973	9	0	9	7	77.8	26.24	CV
1974	5	2	7	3	42.9	34.03	CV
1972[4]	8	0	8	8	100	–	RV
1973[4]	3	0	3	3	100	–	RV
1974	1	1	2	1	50	–	RV
1974	5	0	5	5	100	–	DV

[1] Data from Weston (1969)

[2] Data from Smith and Murphy (1973)

[3] Data from J. R. Murphy (pers. comm.) Less time was spent in the field during the 1971 nesting season than the other years here listed.

[4] Data from R. Ferris (unpubl. field notes)

[5] Abbreviations: CV = Cedar Valley, RV = Rush Valley, DV = Dugway Valley

the same nest, perhaps a victim of cannibalism. Two of three young were lost in another nest, the second 11 days after the first. The nestling mortality in 1974 was 57 percent.

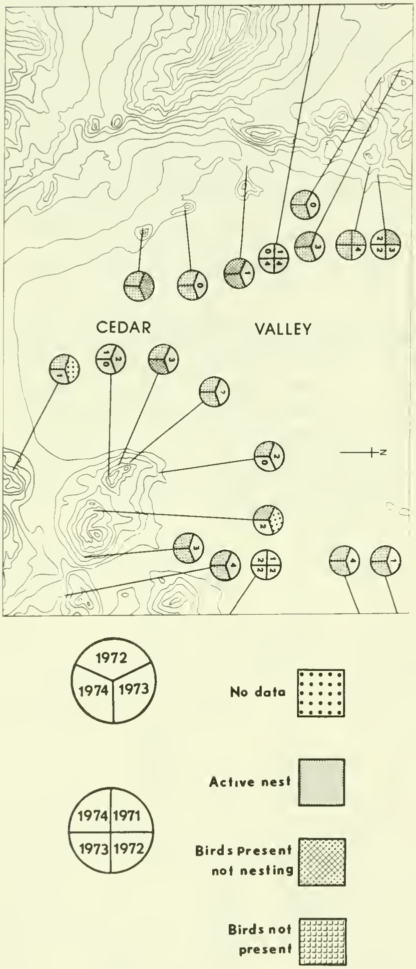

Fig. 2. Ferruginous Hawk nesting territories and young fledged, 1971-1974. Numbers within the sections of each circle represent the number of young fledged for that year.

Nest desertion.— None of the nests visited during the study were deserted by the nesting pair. However, visits were not made prior to laying or during incubation periods in two of the three nesting seasons. In 1973 regular visits were made to three nests during incubation. Although these nests were not deserted, our presence probably contributed to their failure (see previous section).

Renesting.— There were no renesting attempts during the study. In all cases when nests failed the pair continued to occupy the nesting territory. A visit to the territory after nest loss would still elicit normal nest defense behavior, although the degree of intensity was often reduced.

Fledging Success.— The number of young fledging declined drastically from a high of 31 in 1972 to 7 in 1973 and only 3 in 1974. Figure 3 summarizes these and oth-

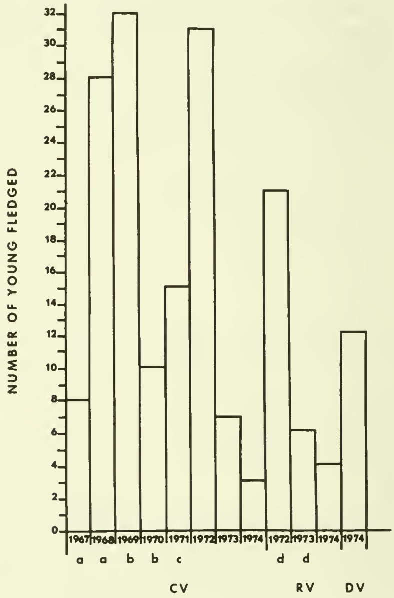

Fig. 3. Number of young fledged per year in Cedar, Rush, and Dugway valleys, 1967-1974.

[a] Data from Weston (1968)

[b] Data from Smith (1971)

[c] Data from J. R. Murphy (pers. comm.)

[d] Data from R. Ferris (unpubl. field notes)

Abbreviations are CV = Cedar Valley, RV = Rush Valley, and DV = Dugway Valley er data for an eight-year period. The number of young fledging per nesting attempt ranged from 1.9 in 1972 to 0.7 in 1973, and 1.0 in 1974 (Figs. 2 and 4).

Figure 4 gives the number of nests fledging one, two, three, and four young, respectively. In 1969 and 1972 the number of nests fledging three or four young was much greater than the number fledging one or two. In 1973 and 1974 the reverse was true; in fact, the maximum number of young fledged from any nest in these two years was two.

AGE OF JACKRABBITS TAKEN AS PREY.— Measurements of jackrabbit hind feet taken from nests were compared with tables in Haskell and Reynolds (1947) to determine ages (Fig. 5). The age distribution was trimodal. Thirty-one (44 percent) of the 71 rabbits were from 2 to 6 weeks old, 32 (45 percent) of the total were from 8 to 12 weeks of age, and 7 (10 percent) were 16 weeks or older. Of the total rabbits found in Ferruginous Hawk nests, 90 percent were 12 weeks old or younger.

Figure 6 gives the age distribution of road-killed rabbits during June, July, and August of 1974. Fifty-seven percent of these rabbits were less than 13 weeks of age.

NESTING PHENOLOGY AND JACKRABBIT REPRODUCTION.— Gross et al. (1974) found four reproductive peaks in the black-tailed jackrabbit, the first commencing approximately mid-January and others occurring at intervals of 40 days (Fig. 7). Figure 7 gives the approximate birth dates of these four litters and the average size of each. Superimposed on the graph are important dates in the nesting phenology of the Ferruginous Hawk. It appears that the hawk's nesting period is closely correlated with the reproductive period of the jackrabbit.

DISCUSSION

Commencing with a peak in 1972, black-tailed jackrabbit populations declined throughout the study period. Gross et al. (1974) found that in their Curlew Valley study area, jackrabbit numbers reached a peak in 1970, then declined in 1971 and 1972. Numbers then dropped precipitously in the spring of 1973 (C. Stoddart pers. comm.).

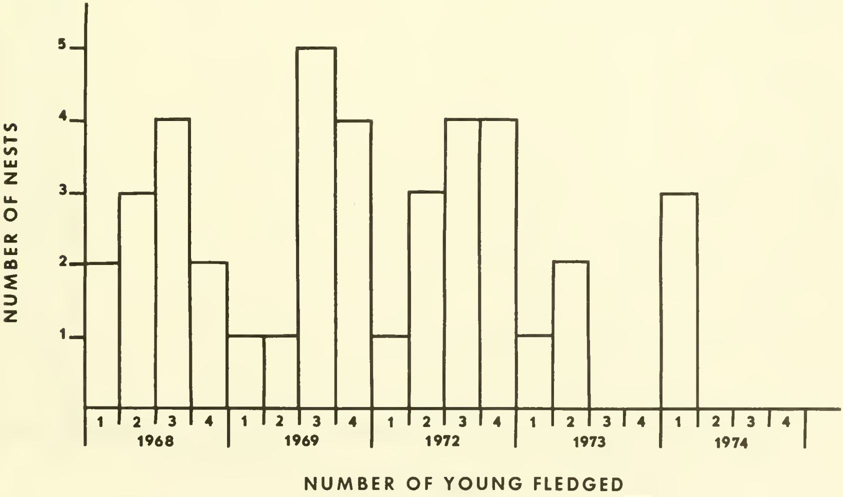

Fig. 4. Number of Cedar Valley Ferruginous Hawk nests fledging 1, 2, 3, and 4 young, 1968-1974.
[a]Data from Weston (Murphy et al. 1969)

We assume that jackrabbit numbers in our study area were similar to those in Curlew Valley, 192 km to the north, prior to 1973, inasmuch as jackrabbits were numerous in 1972 at least on the east side of Cedar Valley. The hawk nests located that year were cluttered with numerous rabbit remains, and hawk production was at its highest point of the study.

Smith (unpubl. ms.) reported a drop in jackrabbit numbers between 1969 and 1970. His observation corresponds closely with those made by Gross et al. (1974).

We observed a decline in rabbit numbers between the 1972 and 1973 nesting seasons. This decline coincided with a fivefold decrease in jackrabbit densities for the same period in Curlew Valley (C. Stoddart pers. comm.). An area of 27,225 m^2 in the eastern portion of Cedar Valley was systematically searched four times for jackrabbits during the 1973 nesting season. Only one rabbit was seen. An active nest near this area had no evidence of rabbit remains. During the 1974 nesting season, transects were made in various parts of the study area (Table 1). Only one area had a density greater than one rabbit per km^2. The number of kilometers per rabbit sighted varied from a high of 0.46 to a low of 8.0 in an area where only one rabbit was sighted during the study. Smith (unpubl. ms.) flushed 4.3 rabbits per km during 1970 (0.23 km/rabbit), the year of lowest jackrabbit densities during his four-year study. This value is twice as large as the comparable one for our study.

In the first eight months of 1974, the number of road-killed jackrabbits was recorded. Over 10,000 km were traveled during this period, and only 122 jackrabbits were seen. The average number of km traveled per jackrabbit was 89.7 (Table 2).

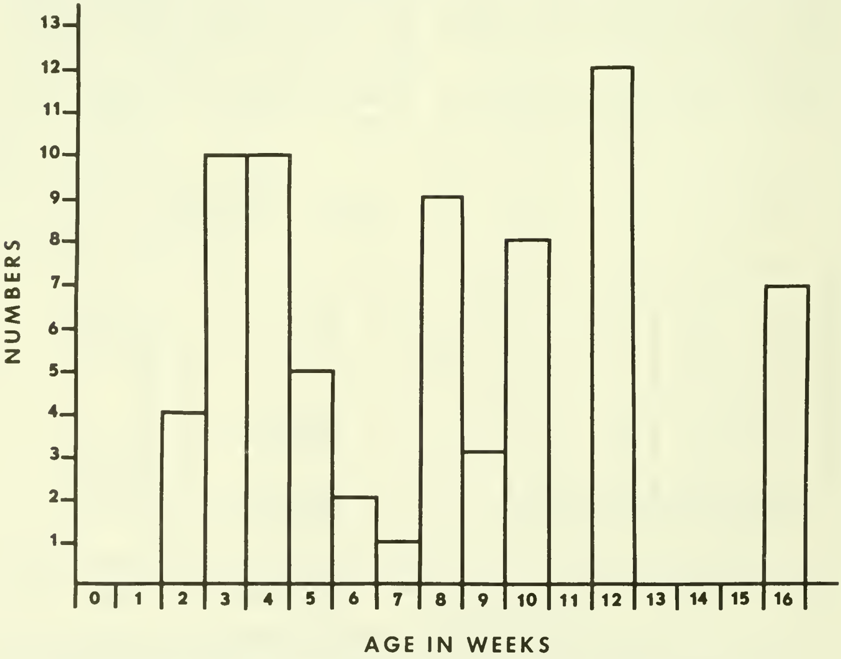

Fig. 5. Number and ages in weeks of jackrabbit prey remains from Ferruginous Hawk nests, 1972-1974.

Adams and Adams (1959) made similar surveys and found the frequency of road-kill per km far exceeded the value we obtained.

Breeding success of the Ferruginous Hawks was higher on the eastern side of Cedar Valley. The western side of the valley, although it does contain some small areas of good rabbit habitat, does not have as much prime habitat as the eastern side. In times of high densities this marginal habitat was utilized by jackrabbits, which in turn allowed hawks to utilize an otherwise unsuitable area.

We believe this helped produce the peak Ferruginous Hawk populations in the late 1960s and early 1970s. We believe that rabbits began to decline first in areas of marginal habitat, where they were most vulnerable to predation, and finally in areas of suitable habitat. Hence, a decrease in rabbit numbers occurred first in the western part of Cedar Valley and then in the eastern sections, producing a similar pattern in the Ferruginous Hawk populations.

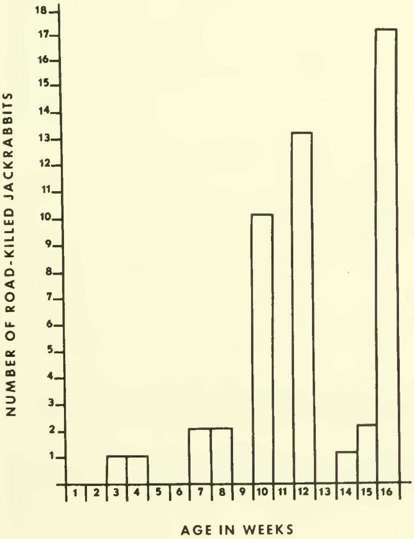

Fig. 6. Age distribution of road-killed jackrabbits, 1974.

Dependence on Jackrabbits.— Weston (Murphy et al. 1969) found that jackrabbits made up a major portion of the Ferruginous Hawk diet. Kangaroo rats were found more frequently as prey remains, but their biomass was not as great as that of the jackrabbits. Howard (1975) found that jackrabbits made up 86 percent of the biomass of the three main prey species. Smith and Murphy (1973) indicated that jackrabbits made up from 93 percent to 95 percent of the prey biomass in their study. In Rush and Cedar Valleys, jackrabbits are used extensively as a food source when young hawks are in the nest. One active nest in Rush Valley in 1972 contained the remains of at least 24 rabbits. In 1973 no active nests were found in Rush Valley.

Alternate Prey Species.— Ground squirrels were scarce in both valleys. Only three white-tailed antelope ground squirrels *(Ammospermophilus leucurus)* were seen in the two valleys over the entire study period. Townsend ground squirrels *(Citellus townsendii)* were more common, but scarce. Jackrabbits made up the only plentiful mammalian prey. When a decline in rabbit numbers occurred, alternate prey was thus not available in sufficient numbers for the hawks to maintain their numbers, and the evidence indicates that the decline we have outlined is due to the drop in jackrabbit numbers.

Townsend ground squirrels were more numerous in Dugway Valley, which is approximately 85 km west of Cedar Valley. Prey populations in this valley were not quantitatively sampled but ground squirrels were evident in large numbers during each visit to the area, and Ferruginous Hawks were correspondingly more successful as nesters. There, only three (20 percent) of 15 nestling hawks failed to fledge. One nest failure accounted for two of these three deaths. The nesting success of the Dugway Valley hawks was evidently due to the presence of a broad prey base. Therefore, our results, perhaps, apply only to areas where jackrabbits are the staple food of this hawk.

Population Dynamics.— From 1968 to 1974, the numbers of pairs of Ferruginous

Hawks in the study area declined steadily (Table 3). In 1972, 16 pairs were present and only one pair failed to nest. In 1973, 9 pairs occupied territories in the intensive study area, and 2 pairs failed to nest. Finally, in 1974 the number of hawks in the study area dropped to 12 individuals—5 pairs and 2 single birds. Two of the 5 pairs failed to nest.

R. Ferris (pers. comm.) documented a similar decline in Ferruginous Hawk numbers in Rush Valley (Table 3). Swartz et al. (1973) observed an increase in the number of nesting pairs of Rough-legged Hawks *(Buteo lagopus)* in Alaska, from 35 pairs in 1968 to 82 pairs in 1970; then the number of nesting pairs plummeted to 10, and only 2 young were fledged in 1972. Tubbs (1974) documented a similar decline in the Common Buzzard *(Buteo buteo)* in Great Britain. In these studies, as in ours, prey numbers declined drastically prior to the decline of raptor populations. The data imply a direct correlation between predator and prey fluctuations.

Habitat Vacancy.— In general, birds of prey occupy the same nesting territory for more than one year (Craighead and Craighead 1969). Nesting territories can thus be conveniently checked each year in the early spring and throughout the year for the presence of nesting birds. In 1972, 16 nesting territories were occupied. Only 9 territories were occupied in 1973, and 7 in 1974. The number of territories that were occupied declined each year, and previously active nesting territories were vacant (Table 3). Keith (1966) outlined the extent of vacant habitat of snowshoe hares *(Lepus americanus)* during a decline. A similar phenomenon of previously occupied habitat being vacant occurred with the Ferruginous Hawk in our study area (Fig. 2).

Davis et al. (1969) found that woodchucks

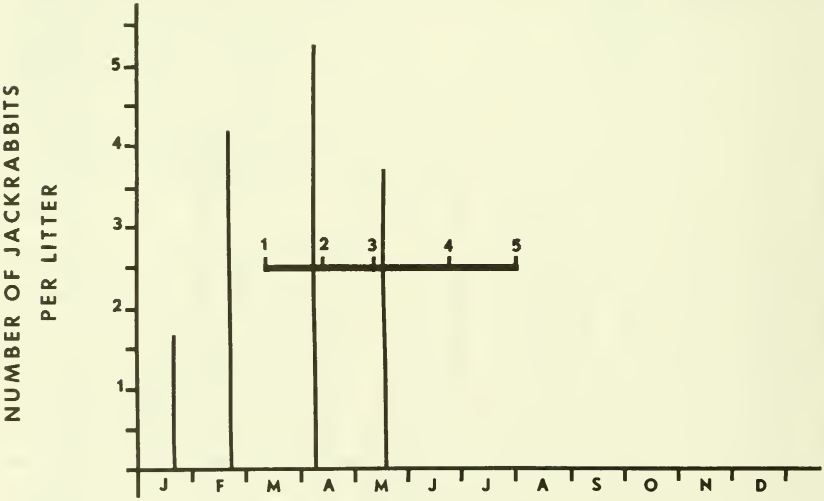

Fig. 7. Number and mean litter sizes of jackrabbits in Curlew Valley, with important dates in Ferruginous Hawk nesting cycle. Vertical lines represent jackrabbit litters. The horizontal line gives important events in Ferruginous Hawk nesting cycle. 1 = territory selection, 2 = mean laying date, 3 = mean hatching date, 4 = mean fledging date, and 5 = mean migration date.

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(Marmota monax) that were removed from one section of their study area were promptly replaced by immature woodchucks apparently from neighboring areas. Carrick's (1963) work with Australian Magpies *(Gymnorhina tibicen)* suggested that a group of unmated birds was present in his study area, and any vacancies in the breeding group were filled by members of this unmated group. Vacant territories were not filled by extra individuals nor was a group of nonbreeding birds observed in the present study with the Ferruginous Hawk.

Although 31 young were fledged in 1972, no young hawks were seen in the study area in 1973. Whether young hawks return to the place of their birth their first year is not known. Mortality rates for this period are also unknown. Craighead and Craighead (1969) suggested that as many as 88 percent of young hawks may die their first year. Hickey (1952) found annual mortality to be approximately 59 percent in yearling Marsh Hawks *(Circus cyaneus)* and 30 percent for the adults. Based on production of the previous year, even if mortality rates were as high as those listed here, a stable population size could be expected. We suggest that prey densities rather than mortality are responsible for the 1973 and 1974 population declines.

In 1972 all of the birds present on the east side of Cedar Valley nested and successfully fledged young, while at least three pairs on the west side did not. One pair on the west side of the valley did not nest. Two pairs that laid one and two eggs, respectively, did not hatch young.

In 1973, three pairs were present on the west side of the valley. One pair fledged two young, one pair failed to nest, and the other pair's nest was blown from the tree. On the east side of the valley four pairs were present, plus a single bird. Though all four pairs built nests and laid eggs, over 50 percent of the eggs failed to hatch and only four young were fledged from these four nests.

In 1974 four nest sites were occupied on the west side of the valley. One pair laid one egg, but none of the other birds laid eggs, although some nest building occurred. In the same year on the east side of the valley two pairs and one single bird occupied territories. Each of the pairs successfully fledged one of the three young that hatched in each nest.

Clutch Size.— The average clutch size was 2.7 in 1972, 2.1 in 1973, and 2.4 in 1974. The overall average of 2.4 is lower than the 3.3 average reported by Weston (Murphy et al. 1969) and Smith and Murphy (1973). Platt (1971) reported an average clutch size of 3.5 for 11 pairs of Ferruginous Hawks in Curlew Valley, and Howard (1975) reported an average clutch size of 2.78 and 2.77 for 1972 and 1973 in the same area. His method of gathering clutch size data was similar to that of our study.

Smith and Murphy (1973) found that clutch sizes vary from two to four eggs. Olendorff (1973) and Howard (1975) reported clutch sizes from one to five eggs. Clutch sizes of from one to four eggs were observed during this study. Clutches containing one and two eggs occurred frequently in areas of low prey numbers. Howard (1975) found 11.6 percent of the clutches examined contained only one egg, but correlation was not made between these nests and prey densities; the data imply that one- and two-egg clutches were correlated with low prey densities.

Fledging Rate.— The number of young fledged per year declined over the study period (Fig. 3). Thirty-one young successfully fledged in 1972, an average of 1.9 per active pair. This value dropped to one young per active pair in 1974; however, there were only three active pairs (Table 1). The overall average fledging rate was 1.2. The number of nests fledging two or more young decreased over the study period (Fig. 4). The reduction of young fledged per nesting pair was evidently correlated with a reduction in prey numbers.

Nestling Mortality.— The low prey abundance was an important factor in nestling mortality. The female from one nest was observed 5.2 km away actively hunting at a time when normally she should have been at the nest brooding the young. Nests were visited periodically after hatching occurred. On a few occasions two nests containing small young were visited, but no adult birds were observed. Howard (1975) also examined nestlings without observing the adult birds in the area. On one occasion we observed a Swainson's Hawk *(Buteo swainsoni)* coursing low over an active Ferruginous nest, but no adult Ferruginous Hawks were observed. The absence of adults from the nest at this time was unusual, as almost always when a nest was approached at least one bird and usually two would begin to display and defend the nest as soon as the investigator left his vehicle.

This apparent nest inattentiveness would enhance the chance of chick mortality both from predation and exposure. We suggest that the high nestling mortality rate in 1973 (43 percent) was due in part to this behavior. The behavior resulted, we feel, from the additional pressure placed on the female hawk to provide herself and young with food, since the male was unable to provide adequate amounts.

C. White (pers. comm.) found that Rough-legged Hawks on the Alaskan tundra were not attentive at the nest when prey density was low. On one occasion he saw a Golden Eagle eating young Rough-legged Hawks at the nest while the adults soared over the tundra some distance away.

The nestling mortality in 1974 was 57 percent. During this nesting season, three nests hatched a total of seven young and fledged only three.

Responses to Lower Prey Densities.—Pairs in areas of low prey densities either failed to nest or laid smaller clutches. Single birds, although they occupied nesting territories, did not mate during the nesting period. In those pairs that laid larger numbers of eggs, the female as well as the male was forced to spend periods away from the nest to supply food for the young. As a result, in many cases, the number of eggs hatched and young fledged was low.

Otteni et al. (1972) found that Barn Owls *(Tyto alba)* raised 1.5 times as many young per pair in years when prey was abundant as in years when prey populations were more limited. McInvaille and Keith (1974) reported a numerical increase in a Great Horned Owl *(Bubo virginianus)* population in response to a cyclic increase of snowshoe hares. Shelford (1943) observed that the population of Snowy Owls *(Nyctea scandiaca)* in the Arctic is directly dependent upon the abundance of lemmings (*Lemmus* spp. and *Dicrostonyx* spp.). During years when lemming populations were low, the owls failed to nest or laid only one or two eggs. In years of high prey populations the percentage of owls nesting was high, and each pair raised many young (maximum of 12). Pitelka et al. (1955) recorded similar correlations for Snowy Owls and Jaegers *(Stercorarius spp.)*. Southern (1970) found that the percentage of Tawny Owls *(Strix aluco)* that nested during low prey years was near zero; however, in years of abundant prey, nearly 100 percent of the owls nested.

Murphy (1975) found that the Golden Eagle population in central Utah experienced a decline in numbers of nesting pairs during the period of this study. He suggested that there was strong evidence to indicate that this trend was also related to population fluctuations of the black-tailed jackrabbit.

Howard (1975) also reported a decline in Ferruginous Hawk numbers and attributed it to a drop in jackrabbit numbers. We suggest that the Ferruginous Hawk responds to fluctuations in prey densities in a similar fashion to the other species discussed above.

Nest Abandonment and Renesting.—Olendorff (1973) and Powers et al. (1973) suggested that Ferruginous Hawks are quick to abandon their nests if disturbed during nest building or incubation. In 1967, Weston (Murphy et al. 1969) reported that three nests containing eggs and four nests ready for eggs were abandoned early in the nesting season after only one visit to each nest. The next year, although identical nest observation procedures were conducted, no nests were abandoned.

We visited three active nests regularly during the 1973 nesting season. None of these three nests was abandoned, nor did we observe any nest abandonment during the entire study. However, the young of two of these nests were destroyed by something. We feel that our presence at the nest was probably responsible to a large degree for these deaths, because some carnivores are known to follow human tracks. Willis (1973) reported the destruction of Ant Bird *(Gymnopithys bicolor)* nests by predators after a routine visit. Ray (1968) suggested the use of napthalene crystals around the nest and on paths to destroy the scent trails made by the investigator. Olendorff (1973) outlined methods of handling and times and duration of visits that will have the least injurious effect on the research subjects. An investigator would be wise to contemplate the impact of the study on the population prior to commencing his or her work. The methods outlined in the references above may be valuable research tools that could decrease the amount of investigator-caused losses to young birds.

Many raptors will lay a new clutch of eggs if all eggs are taken shortly after completion of the clutch (Olendorff 1971). No renesting occurred during this study even though several nests were destroyed, including one nest that was blown out of a tree shortly after the time when the clutch should have been completed. The pair from one of the aforementioned nests that had successfully hatched three young, only to have them destroyed, moved 0.4 km east and defended an alternate nest site. Less than a dozen sticks were piled on top of a rock at this new location. Despite this, the pair actively defended this token nest.

Age of Rabbits Taken as Prey.— The hind legs of 71 jackrabbits were collected from active nests throughout the study. The length of the hind foot was compared with tables in Haskell and Reynolds (1974) to determine age. A trimodal distribution was noted (Fig. 5). Thirty-one (44 percent) of the 71 rabbits were from two to six weeks old, 32 (45 percent) of the total were between eight and twelve weeks of age, and 7 (10 percent) were sixteen weeks or older. Of the total rabbits found in Ferruginous Hawk nests, 90 percent were less than thirteen weeks of age. Similar results were reported by Dunnet (1957) in Australia where avian predators were selectively killing young rabbits. He found that when the rabbits reached three months of age they were no longer vulnerable to the intense avian predation to which they had been subjected earlier.

The adult Ferruginous Hawks were clearly utilizing the immature jackrabbits to a much greater degree than the older rabbits. This is not surprising, because during the nesting season there are more immature than mature rabbits available to the hawks, and the young rabbits would undoubtedly be easier to catch, kill, and carry.

Nesting Phenology and Jackrabbit Reproduction.— Gross et al (1974) found four reproductive peaks in the black-tailed jackrabbit, the first commencing approximately mid-January and others occurring at intervals of 40 days (Fig. 7). The first two litters are born prior to the selection of territories by the Ferruginous Hawks. In some cases the hawks do not even return to the nesting area prior to the birth of these two litters. During years of good rabbit production, litters one and two should provide an abundant prey source for the courting hawks. After the nest has been constructed, egg laying begins (Fig. 7). During egg development an ample supply of prey may be as important as when young are in the nest. Average clutch sizes from years of good rabbit numbers are larger than those calculated for years of low rabbit numbers (Smith and Murphy 1973).

The average clutch size for 1972 was 2.7, but for 1973 and 1974 it was 2.1 and 2.4, respectively. In 1972 one nest on the west side of Cedar Valley contained a single egg, another only two eggs. In both cases hatching did not occur. Also, a pair in this same area failed to nest. There is a general lack of good rabbit habitat on the west side of the study area. Data for years other than 1972 indicate fewer rabbits in this area than the eastern side of the valley. Although the data do not unquestionably support the thesis that fewer eggs are laid when prey is scarce during periods prior to egg development, it appears that such a trend did occur in this study as well as in the investigation conducted by Shelford (1943) on the relationship of Snowy Owl response to low prey densities.

We suggest that the timing of the arrival of the Ferruginous Hawk in its nesting territory is correlated with the presence of a suitable prey base in the form of coinciding litters of rabbits that are available for prey during prelaying activities. Rabbit litter three is born just prior to egg laying by the hawks. This is the largest of the three litters, averaging 5.2 young per pregnant female (Gross et al. 1974). During incubation in many raptor species the female hawk does most of the brooding and the male supplies her with food (Brown and Amadon 1968). If the male has little trouble supplying both himself and his mate with food during this period, the female apparently needs to leave the nest infrequently during the incubation period. A large number of young jackrabbits of approximately 1 to 12 weeks of age would be available to a Ferruginous Hawk pair that occupied a suitable territory throughout the period of incubation during a year of good rabbit densities. This presumptive age distribution compares favorably with the distribution of the ages of rabbits actually taken from the nest (Fig. 5). Members of the first litter would be approximately 12 weeks of age at the time of laying and would still be available to the hawks during incubation.

Shortly after hatching, rabbit litter four is born. Litter three would be approximately four weeks of age, and litter two approximately twelve weeks of age at this time. The three largest litters are thus available for food as the young hawks develop. The members of litter four are less than five weeks of age while the young hawks are in the nest. Based on ages of rabbits taken to the nest, three of the four litters (litters 2, 3, and 4) are available for use as food for the nestling hawks. The last two litters probably provide the majority of the rabbits utilized as prey during hawk development.

After the young hawks leave the nest they remain in the area for approximately one month prior to migration. Rabbit litter four is approximately 10 weeks old at this time, and probably provides the major portion of the food supply of the young hawks. Young hawks likely cannot catch adult rabbits or even young of that year other than members of litter four. The timing of departure could well be correlated with a decline in available prey. Data from rabbit transects made during the nesting season in 1974 indicate that this may be so, inasmuch as jackrabbit densities declined throughout the nesting season.

Other raptors migrate at approximately the same time as the Ferruginous Hawk (August 1). A. Jenkins (pers. comm.) noted a peak in migrating hawks along the Wasatch Front in late August. Although some buteos were observed, most migrants were accipiters and falcons. Olendorff (1973) recorded the Ferruginous Hawk as a resident species in the Pawnee Grassland of Colorado. It is not known why this species should be migratory in central Utah, yet resident in a location only about 800 km to the east. In both locations an influx of wintering raptors occurs, primarily Rough-legged Hawks and Bald Eagles *(Haliaeetus leucocephalus)*. In Utah the Ferruginous Hawks have migrated before these species appear. Competition does not seem, then, to be the factor of importance. We suggest that perhaps prey availability dictates time of migration. Further light could be shed on this hypothesis if more were known about the wintering areas and food habits of the Ferruginous Hawk.

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A NEW SPECIES OF *RHOPALOMYIA* (DIPTERA: CECIDOMYIIDAE) FROM *ARTEMISIA LUDOVICIANA* NUTTALL (COMPOSITAE) IN UTAH

Raymond J. Gagne[1]

ABSTRACT.— *Rhopalomyia (Diarthronomyia) subhumilis* Gagné, a new species of *Artemisia ludoviciana* Nuttall (Compositae), is described and its taxonomically important structural features illustrated. The new species is compared to its most similar North American congeners.

This paper provides a name for a species of *Rhopalomyia* whose biology is treated in a companion paper by Ranasinghe (1977). As pointed out in Jones, Gagné, and Barr (in press), *Rhopalomyia* species are so numerous and the structural differences so few and so slight that the species do not lend themselves well to description without biological data. That condition is met for this new species by the information in Ranasinghe (1977).

Rhopalomyia subhumilis n. sp.

MALE.— Wing length, 2.2-2.5 mm. Eyes separated at vertex by less than diameter of 1 eye facet. Antenna with 14-16 flagellomeres; neck flagellomere III, 0.50-0.86 times length node; neck V, 0.60-0.88 times length node; neck VII, 0.64-0.90 times length node. Fused labellae (Fig. 6) with ventral notch in frontal view, 0-4 setae per side. Palpus (Fig. 6) 2-segmented: segment I as wide as long, with 1-5 setae; segment II as long as I but tapered apically, with 1-3 setae. Frontoclypeus with 6-9 setae per side. Anepisternum with 4-8 setae. Claws toothed (Fig. 7). Empodia as long as claws. Abdomen: tergum III with 8-22 setae per side, tergum V with 13-26, VII with 13-20 and occasional scales, and VIII with 8-20, the two groups on VII united mesally or separated by short distance; pleura with scales, 0 setae; sterna II-VII each with basal pair of trichoid sensilla, sternum VII with basal setal group continuous across sclerite. Terminalia (Figs. 3-5): basimere stout with short ventral lobe; telomere short-ovoid, the tooth wide; sternum X concave apically.

FEMALE.— Wing length, 1.8-1.9 mm. Antenna with 15-16 flagellomeres; flagellomere necks not defined or very short to VI, undefined beyond VI. Other head and thoracic characters as in male. Abdomen: tergum III with 12-14 setae per side; V with 13-18, and VII with 5-12, the two groups on VII barely divided; pleura and sterna as in male; tergum VII 0.23-0.26 times length distal half of ovipositor.

PUPA.— Head (Figs. 1-2): antennal horns strongly developed, acutely pointed; frons with two prominent, pointed protuberances. Pronotum convex, not prominent, the two setae long.

HOLOTYPE, male, ex subterranean stem galls on *Artemisia ludoviciana* Nutt., Philadelphia Flat, 12 mi. E Ephraim, Sanpete Co., Utah, 9-VII-1975, R. B. Farnsworth, USNM Type No. 66621. Paratypes: 14 males, 23 females, same data as for holotype; 2 males, 6 females, same data as holotype, except collected 10-VII-1976, S. K. Ranasinghe. Other material: pupal exuvia and galls associated with above collections. Representative collections of males, females, and pupal exuvia in Life Science Museum, Brigham Young University and California Academy of Sciences. Remainder of material in USNM.

REMARKS.— *Rhopalomyia subhumilis* belongs in the subgenus *Diarthronomyia* as do all other *Rhopalomyia* that occur on *Artemisia* and *Chrysanthemum*. The dis-

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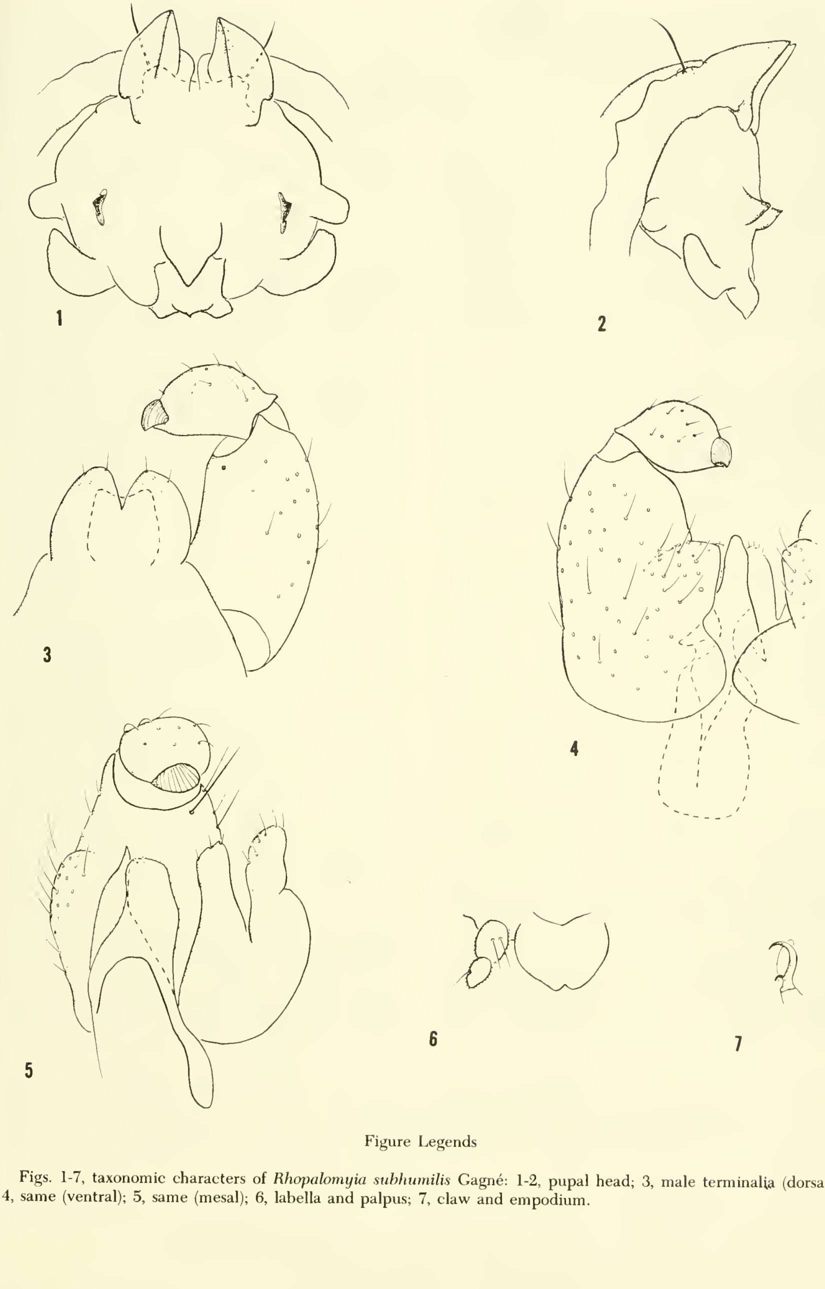

Figure Legends

Figs. 1-7, taxonomic characters of *Rhopalomyia subhumilis* Gagné: 1-2, pupal head; 3, male terminalia (dorsal); 4, same (ventral); 5, same (mesal); 6, labella and palpus; 7, claw and empodium.

tinguishing structural feature uniting these species is the lack of all but caudal setae on the abdominal terga. The new species differs from all other Nearctic species of *Diarthronomyia* by the following combination of characters: palpus two-segmented, claws toothed, male basimere with ventral lobe, male telomere short, with wide apical tooth, pupal head with frontal protuberances and strongly developed antennal horns. *Rhopalomyia subhumilis* will not run past couplet 5 in the key to 23 species of *Rhopalomyia* on *Artemisia tridentata* (Nuttall) in Jones, Gagné, and Barr (in press). The pupal head will readily distinguish this species from the other keyed *Rhopalomyia* having 2-segmented palpi and toothed claws. Of the 9 other Nearctic *Rhopalomyia (Diarthronomyia)*, only *R. gnaphalodis* Felt from a woolly leaf gall of "*Artemisia gnaphaloides*" and *R. chrysanthemi* from a conical gall on green tissues of *Chrysanthemum* spp. have two-segmented palpi and toothed claws, but the pupal antennal horns are much more attenuate in both species, and the male telomere of *R. chrysanthemum* is much longer than in *R. subhumilis*. The name "subhumilis" means "subterranean".

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BIONOMICS OF A SUBTERRANEAN GALL MIDGE (DIPTERA: CECIDOMYIIDAE) FROM *ARTEMISIA LUDOVICIANA*[1]

M. A. S. K. Ranasinghe[2]

Abstract.— Bionomics of a gall midge that emerged from nodulelike structures of herbaceous sage, *Artemisia ludoviciana*, was studied as a part of a larger investigation on possible nitrogen fixation by this plant. Infested plants collected from the field were regularly examined in the laboratory where some of them were grown in a liquid nutrient medium. In the laboratory, adult midges were reared from pupae and induction of infestation was attempted. Apparent nodulation of these plants is caused by the subterranean bud galls of a previously unknown gall midge, *Rhopalomyia subhumilis* Gagné. Life history of this midge is reported. These midges have one generation per year in the study areas and overwinter as larvae. There were no indications of paedogenesis. These midges are parasitized by a species of Platygasteridae.

Apparent nodulation on the underground parts of an herbaceous sagebrush, *Artemisia ludoviciana* Nutt., was reported by Farnsworth and Hammond (1968) in their investigations on nitrogen fixation by nonleguminous plants. Later, nitrogenase activity, measured through acetylene-ethylene gas assay, was recorded from these nodulelike structures (Farnsworth and Clawson 1972). When midges emerged from the stored mature bodies in the laboratory, it was hypothesized that they might act as vectors of the nitrogen-fixing microorganisms (Farnsworth 1975). It was also possible that the presumptive nodules actually were subterranean galls of a hitherto unknown midge that infested these plants. This study was undertaken to investigate the bionomics of these midges in relation to the nodulelike structures of these sage plants, as a part of a larger investigation of possible nitrogen fixation by *Artemisia ludoviciana*.

The midge that emerged from the nodulelike structures was found to be *Rhopalomyia subhumilis* Gagné, a species previously unknown to science, in the family Cecidomyiidae (Gagné 1977). This large family includes most of the economically important gall midges (Mani 1964). *Rhopalomyia subhumilis* is the only subterranean gall midge reported from *Artemisia*. It is one of the few gall midges known to inhabit the subterranean parts of the host plant.

Artemisia ludoviciana is an herbaceous plant with a perennial, subterranean, rhizomal stem. In Utah, the annual aerial growth of this plant persists from early spring to early fall. This plant is indigenous to much of the United States from western Canada and California eastward to Montana and the Dakotas.

The objective of the present research is to study the life history of this gall midge in relation to the galls of the host plant.

Rubsaamen (1892) erected the cosmopolitan genus *Rhopalomyia* which now contains over 200 known species (Gagné 1974), 56 of which are from North America north of Mexico (Foote 1965). Jones (1971) apparently found an additional 35 species from the *Artemisia tridentata* complex in Idaho, and in relation to this work Gagné (1974) revised the subgenus *Diathronomyia*. Gagné (1975) recognized additional new *Rhopa-*

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lomyia species. He has named and reviewed the taxonomic status of the gall midge reported in this paper (Gagné 1977).

Rhopalomyia species are apparently host specific and they are responsible for a particular kind of gall on some part or parts of the plant (Gagné 1974). Mani (1964) reported that galls of *Rhopalomyia* are largely confined to the Compositae, but a few make galls in plants belonging to other families (Felt 1940). Several *Artemisia* species harbor galls of *Rhopalomyia* (Felt 1940), although none has been reported from *Artemisia ludoviciana*. Most *Rhopalomyia* species show marked preference to flower and bud galls (Felt 1915). *Rhopalomyia thompsoni* Felt was named from the root galls of *Solidago rugosa* (Felt 1907), and *Rhopalomyia hirtipes* O.S. from both aerial and subterranean bud galls of *Solidago juncea* (Felt 1915). Published records of subterranean galls on *Artemisia* were not found, although galls are known to occur on other parts of these plants (Felt 1911b, 1940).

Earlier work on *Rhopalomyia* was mostly confined to records of rearing them from galls and to taxonomic descriptions (Felt 1907, 1911a, 1916). Cockerell (1909) described the biology of *Rhopalomyia betheliana* Ckll. from *Artemisia frigida*, and Lander (1951) reported a short description of an unidentified *Rhopalomyia* species from *Artemisia tridentata* Nutt., in Utah. The ecology of several apparent species of *Rhopalomyia* found on *Artemisia tridentata* complex in Idaho was studied by Jones (1971), and the biology of *Rhopalomyia hirtipes* from *Solidago juncea* was reported in detail by Spence (1969).

Materials and Methods

The study areas are located in the Manti-La Sal National Forest within an elevation range of 2,440 to 3,200 m and between 22 to 30 km southeast of Ephraim, Sanpete County, Utah, where an abundance of host material was available. This study was carried out from May 1976 to June 1977.

In the laboratory, for each gall the location on the host plant was recorded and the diameter was measured using a vernier caliper. Some of the galls were dissected under a stereoscopic microscope to record the number and stage of development of the midges found inside. An ocular micrometer was used for all linear measurements of the gall midges.

The soil-free, infested plants, supported by cotton wads kept on either side of the gallbearing section, were grown in glass tubes (Fig. 1) containing White's liquid nutrient medium (Paul 1970). Each tube was covered with black paper to prevent light penetration.

Adult midges were obtained from the mature galls by keeping them in plastic bags. Once emerged, the adult males and females were separated, their dimensions were recorded, and the midges were preserved in 70 percent alcohol. The adult parasites collected were also preserved in 70 percent alcohol.

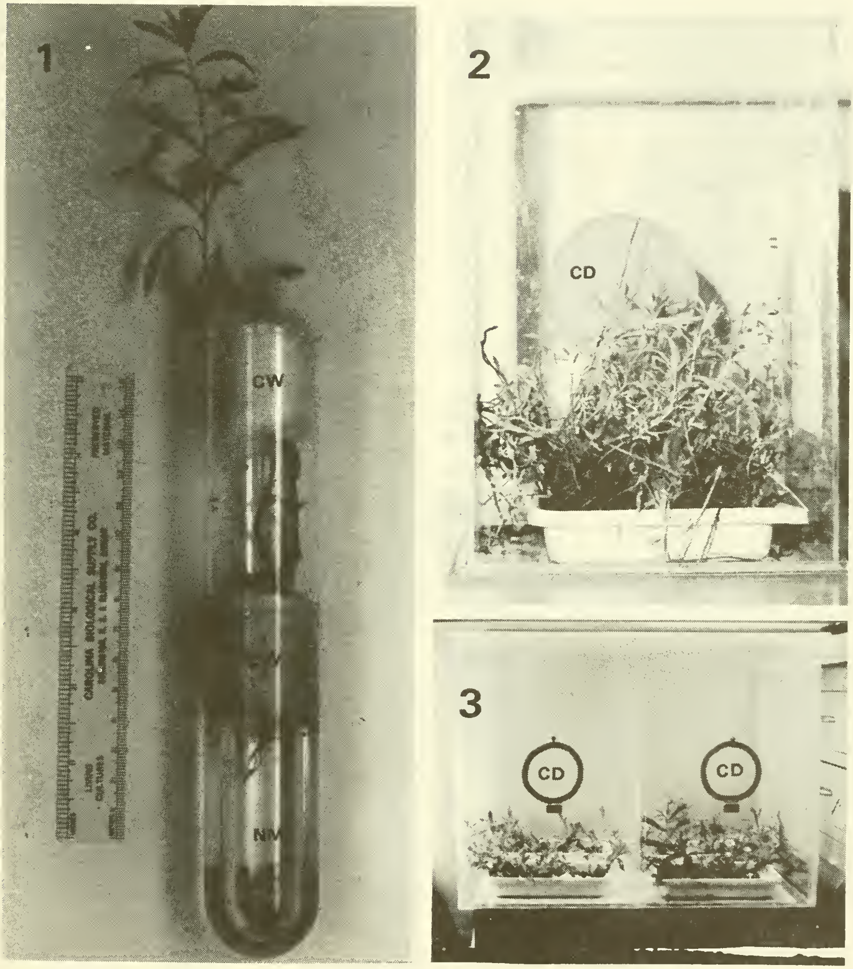
To find whether both the male and female midges emerged from the same gall, 24 mature galls were kept, each in a separate plastic vial (8.0 x 2.5 cm), between cotton wads at the top and the bottom of the vial. Some infested plants were kept intact in rearing chambers (36 x 26 x 26 cm), modified from Spence (1969), to allow observance of the adult behavior (Fig. 2). Some other infested plants were grown in a growth chamber at 35° C and 12 hours of daylight using White's liquid nutrient medium. Induction of the galls in the laboratory was attempted by keeping 24 uninfested plants in one half of a Plexiglas cage with a nylon-mesh-covered window, separated by a removable Plexiglas partition from the other half of the cage containing 24 infested plants (Fig. 3). These plants were grown in plastic trays containing cotton pads moistened with the liquid nutrient medium periodically. The partition was removed once the adult midges emerged and the uninfested plants were exposed to them. Later, these plants were examined for the signs of gall formation.

The photographs were taken using a Honeywell Pentax ® SP 1,000 camera, Vivitar extension tubes, and a Nikon ® stereoscopic microscope with the use of Panatomic ® X or Plux X ® films.

RESULTS

Life History

EGG.— The eggs were first observed in the laboratory on 17 June 1976 but were collected from the field from 24 June to 17



Figs. 1-3: 1, Glass rearing tube with an *Artemisia ludoviciana* plant, CW-Cotton wad, NM-Nutrient medium. 2, Single-compartment midge-rearing cage, CD-Cage door. 3, Twin-compartment midge-rearing cage, CD-Cage door.

July 1976. These eggs were normally found in or near the leaf axils of the lower part of the aerial shoots and rarely on the underside of the leaves. In the laboratory the eggs were found even on the walls of the glass rearing tubes. Eggs were usually found in clusters varying from 12 to 49 eggs per cluster. Nine egg clusters included a total of 205 or an average of 23 eggs per cluster.

The eggs were pale red in color. The average measurements of 45 randomly selected eggs were 0.30 x 0.06 mm. Each egg was cylindrical in shape with tapering ends (Fig. 4). Under laboratory conditions the eggs hatched in three days at room temperature to produce pale red-colored, first instar larvae. In the field the exact time of hatching could not be determined, but on one occasion eggs observed in the field on 7 July at Skyline Drive could not be found during the next visit a week later, indicating that the eggs most likely hatched in less than a week.

Larva.— Earliest laboratory observation of the pale red-colored, first instar larvae was on 19 June 1976. Average measurements of 23 such larvae were 0.27 x 0.06 mm. When examined under the microscope, these larvae were found to crawl on the stem. However, the first instar larvae soon perished under laboratory conditions. In the field similar larvae were recovered from around the basal axillary buds of the shoots. On one occasion discarded pale red-colored larval skins were observed near a newly formed gall.

The first larva to be recovered from a new young gall was found on 8 July 1976 at the Blue Bell area at an elevation of 2,700 m when the soil temperature at a depth of 7 cm was 18° C. These larvae were colorless and translucent. Each of these larvae was confined to a distally tapering larval chamber which was slightly larger than the larva. The average of 33 such larvae measured was 0.35 x 0.23 mm. The midge overwintered in this larval form.

In the following spring few larvae similar to above were still found in the galls on 9 May 1977 at the Blue Bell area, soon after snow had melted. At Skyline Drive (elevation 3,300 m) these young larvae occurred even in the first week of June. At the Blue Bell area these young larvae were inside thin-walled, liquid-containing larval chambers of the galls located at the bases of aerial shoots about 1.7 cm high, growing in soil where the temperature at a depth of 2.5 cm was 8° C. However, by this time some larvae had already begun to develop (Fig. 5).

With the growth of the larva, the size and the wall thickness of the larval chamber increased progressively. But the distal end of the larval chamber remained comparatively thin walled and was oriented away from the basal attachment of the gall to the host plant. The fluid content of the larval chamber gradually decreased with the growth of the larva. No solid materials were found in the larval chambers at any time.

In the laboratory the young, growing larvae kept between the moist filter papers survived only up to three days, probably due to lack of nutrients. Hence the development of a given larva could not be followed through all the different stages by rearing them in the laboratory. Instead, midge galls regularly collected from the field during the growing season were dissected to follow the development of the larvae.

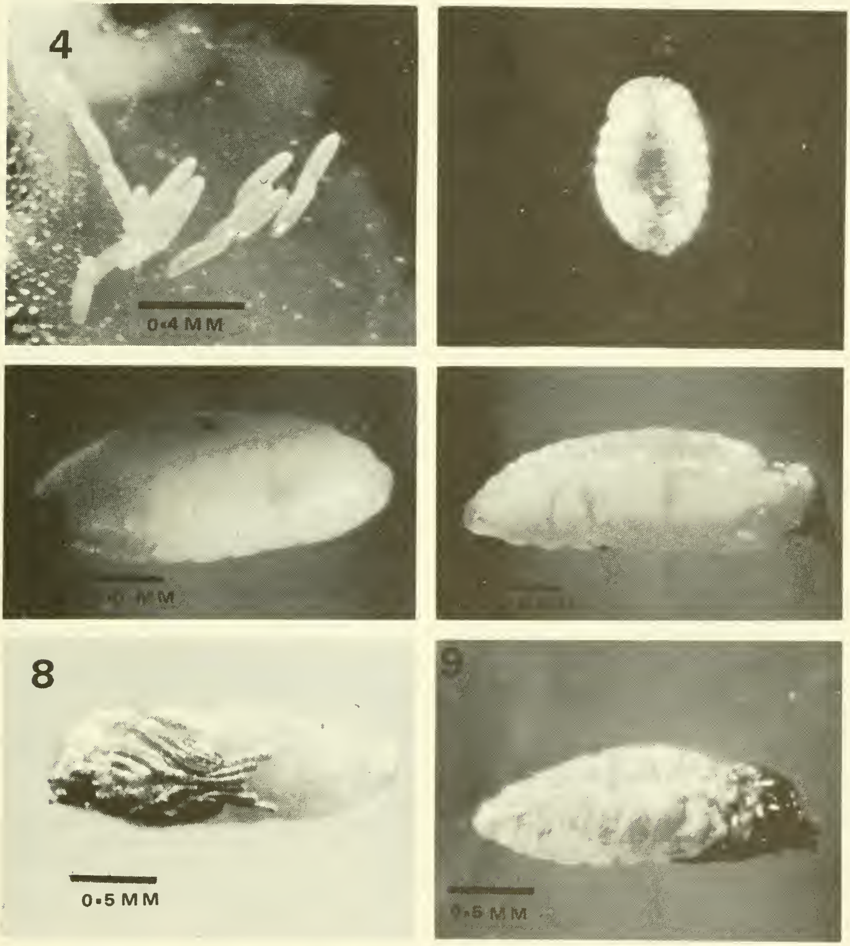
The range and the average of the lengths of the larvae collected from the field during their growing season are shown in Table 1.

Table 1. Larval lengths of *Rhopalomyia subhumilis* from *Artemisia ludoviciana* galls at Philadelphia Flat (1976).

Date	Number of larvae	Length in mm	
		Average	Range
03-VI-76	26	0.54	0.42-1.32
08-VI-76	47	0.78	0.42-1.38
17-VI-76	26	1.30	0.62-2.12
24-VI-76			
26-VI-76	17	1.51	0.81-2.12
01-VII-76	07	1.47	1.00-1.70
09-VII-76	15	1.56	*0.40-2.10

*New young larvae

During this period the length-to-width ratio of the larvae remained about 2:1. The largest larva observed was 2.12 x 1.00 mm. With growth, the originally colorless larva in the young gall changed to white, then yellow, and finally to brownish yellow at maturity. This mature larva (Fig. 6) was opaque compared to the translucent young larva. These midge larvae were rather characterless. The larval body consisted of 13 segments. The head capsule of the young larva was inconspicuous but became more



Figs. 4-9. Developmental stages of *Rhopalomyia subhumilis:* 4, Eggs. 5, Young larva. 6, Lateral view of the mature larva. 7, Lateral view of early pupa. 8, Ventrolateral view of late pupa. 9, Lateral view of female pupa just prior to eclosion.

visible with growth, due to pigmentation. The growing larvae were orientated with their heads toward the bases of the larval chambers until they reached the prepupal stage when their position reversed. The larvae were usually sluggish except for their feeding movements. When kept on a drop of water and subjected to intense light from a microscope lamp they moved away from the light by waves of body contractions.

Pupa.— The appearance of a pair each of antennal and facial horns on the ventral side at the anterior end of the mature larva was the first externally visible sign of pupation. At this time some of the other pupal structures were also visible through the cuticle of the prepupa. The horns were first visible on the laboratory-reared larvae on 9 June 1976, and the pupae were collected at Philadelphia Flat (elevation 2,900 m) on 15 June 1976.

This early pupa was white in color with a slight dorsal curvature of the body at the anterior end (Fig. 7). By the end of the first 24 hours the distal spines of the antennal and facial horns became brown in color, due to pigmentation. The compound eyes, which were white in color, became progressively browner within the first 48 hours, beginning around the ommatidia. On the fourth day a black bar appeared connecting the two eyes on the dorsal side. The eyes became black in color by the end of the fifth day. The pigmentation of the antennae commenced at their distal ends by the third day and then gradually proceeded toward the bases, making the orange-colored antennae entirely black by the end of the fifth day.

The white-colored thorax turned yellow within the first 24 hours and brownish red by the end of the third day. It became brown in color by the end of the fifth day, and by then two black bands appeared dorsolaterally at the posterior end of the thorax. The black coloration of the wing buds and the legs was initiated at their distal ends by the end of the third day and then gradually proceeded proximally to make them entirely black by the end of the fifth day.

The color of the pupal abdomen changed from white to pale yellow within the first 24 hours. In the male pupae this color intensified and then turned yellowish brown in the mature condition. But in the female, pupae the color of the abdomen gradually changed to pale red by the third day and then increased in intensity to become dark red upon maturation. The pupae were completely mature by the end of the sixth day (Fig. 8). The setal bands of the adult were visible through the pupal case just before eclosion, and the ovipositor in the female pupa was apparent by this time (Fig. 9).

The average length of 10 randomly selected mature male pupae was 1.92 mm, and that of 10 female pupae selected at random was 2.11 mm. In addition to this size difference the female pupae could be distinguished from the male pupae by the red-colored abdomen and comparatively shorter legs which extended only up to the end of the fifth abdominal segment. In contrast, the male pupae had a yellowish-brown abdomen and longer legs, which extended up to the end of the seventh abdominal segment.

I was able to rear the pupae from the first day of pupation to the adult stage by keeping them between moist filter papers in petri dishes at room temperature. The first adult emerged in the laboratory on 16 June 1976. Duration of the pupal stage varied from six to seven days in the laboratory at room temperature. In the field, pupal exuvia were first observed on 24 June 1976 at the Blue Bell area when soil temperature was 18° C at a depth of 6.0 cm.

Adults.— Immediately prior to eclosion the mature pupa became periodically active with bending movements of the body. The first signal of eclosion was the appearance of a longitudinal split along the mid-dorsal line of the pupal thorax. This thoracic split widened, exposing the adult thorax, and the adult head protruded through it with the eyes followed by the bases of the antennae. The white-colored adult thorax, bearing four dorsal bands of hair, emerged with the prothoracic legs coming out next and the halteres becoming free before the wings

(Fig. 10). Once the head and thorax were free, the adult apparently paused for a few seconds and then vigorously wriggled to free the abdomen from the pupal case. During eclosion the shaking of the free parts of the body perhaps helped to draw the encased parts out of the pupal case. In the laboratory eclosion was completed in 11 minutes for this pupa which was reared in a petri dish. The examination of the pupal exuviae indicated a similar process of eclosion under the field conditions. The pupal exuviae remained protruding out of the cavities of the gall surface (Fig. 11).

The adults emerged in the laboratory on 16 June 1976. In the field adult emergence occurred from 24 June 1976 (lower elevations) to 17 July 1976 (higher elevations). Adults were collected until 5 August 1976 from the infested plants reared in a growth chamber. When these plants were allowed to continue inside the growth chamber, five more adults emerged from the galls on the new shoots; they presumably belonged to a second generation. But no second generation adults were collected from the field.

Laboratory observations on 106 adults gave a male to female sex ratio of 1:1.9. Twenty-five randomly selected males averaged 1.76 mm in length, within a range of 1.28 to 2.12 mm. For 25 randomly selected females the average length was 1.96 mm within a range of 1.54 to 2.30 mm. These measurements were taken from the anterior end of the head capsule to the end of the last abdominal segment, exclusive of the antennae and the terminalia. The adult male has a yellowish-brown abdomen, comparatively long legs and a short pair of claspers (Fig. 12). The female could be recognized by her shorter legs, broad, red-colored abdomen, and the long ovipositor (Fig. 13). A complete description of the adults is presented by Gagné (1977).

Gravid females isolated from the males did not oviposit even after three days, but when adults of both sexes were present together they laid the eggs during the first day after emergence. I did not observe the act of mating, but it presumably took place shortly after emergence and lasted for a brief period of time.

Prior to oviposition the female probed over the host plant, apparently to select a suitable site. During oviposition the female was found near a leaf axil with her ovipositor extended. The longitudinal axis of her body was orientated to make a narrow angle with the stem. The prothoracic legs grasped the stem and the other legs supported the body. The metathoracic legs were observed to shake vigorously at intervals. The ovipositor was inserted into the leaf axil and the abdomen contracted periodically, accompanied by the wriggling movements of the ovipositor. This oviposition lasted four minutes in the laboratory.

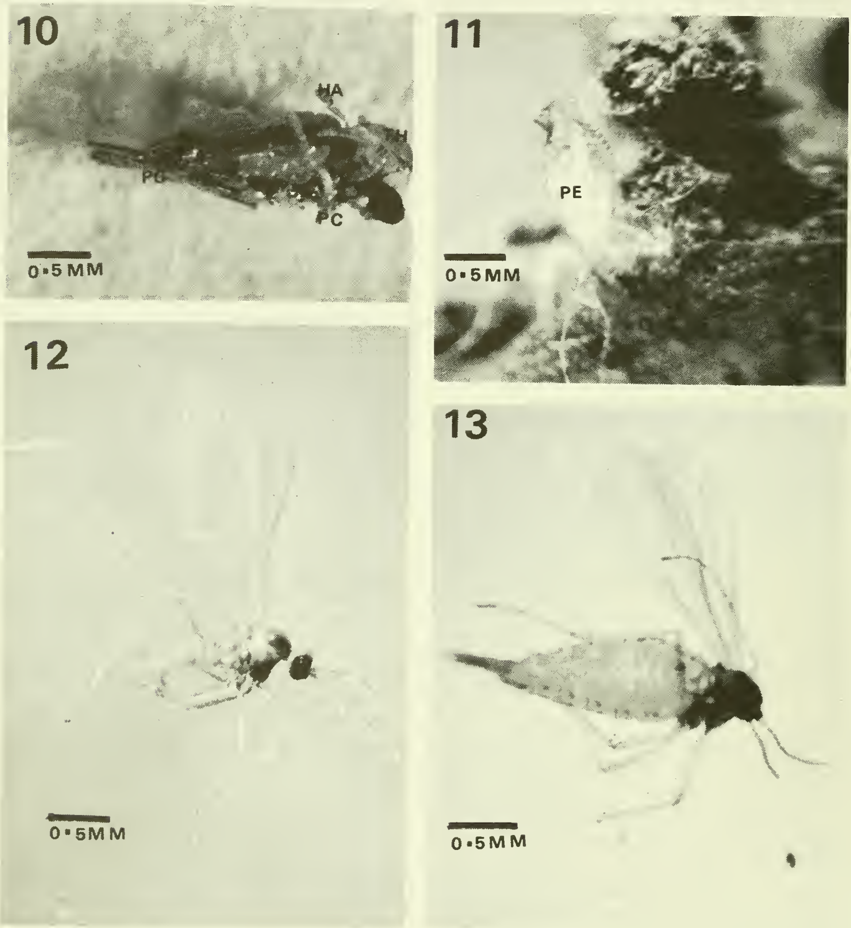
The adults were never observed to feed, and their mouth parts were vestigial. The males were very active on the first day after emergence and they flew rapidly. They became lethargic and died on the second day. The females usually walked over the host plants after emergence and invariably rested for a few hours underneath the leaves (Fig. 14). They did not fly as swiftly as the males, but were still active on the second day after emergence. The females lived up to three days in the laboratory.

PARASITES

Twenty six of the 160 midge larvae, or 16.2 percent of the larvae examined, were parasitized by an undetermined species of Platygasteridae. However, this sample included 45 very young larvae, smaller than 0.5 mm, at which stage it was difficult to detect the presence of parasites. This parasite apparently laid its eggs on the midge eggs. The larvae of the parasite were first observed on 3 June 1976 when the host larvae had already begun their development in the larval chambers. I never observed more than one parasite per larval chamber. Either all of the larvae were found in a gall or only part of them were parasitized.

The larva of the parasite was invariably found on the midge larva. The earliest parasite larva observed inside a midge larval chamber measured 0.3 x 0.06 mm. It was quite active compared to the lethargic midge larva and moved away from light. The host larva was not attacked until the parasite larva reached an advanced stage. The parasitized midge larvae were apparently more fragile and damaged easily during handling.

The parasite larva remained colorless up to its maturation, and just prior to pupation it bored into the midge larva near its anterior end. The first pupa of the parasite was observed on 30 June 1976. Six of these averaged 1.6 x 0.8 mm in dimensions (Fig. 15). The first adult parasite emerged on 18



Figs. 10-13: 10, Eclosion of the adult, HA-Haltere, PC-Pupal case, TH-Adult thorax. 11, Pupal exuvium protruding out of the gall surface, GA-Gall, PE-Pupal exuvium. 12, Lateral view of the adult female (ovipositor retracted). 13, Lateral view of the adult male.

June 1976 and they continued to emerge until 5 August 1976.

I did not observe any inquilines in the 77 galls dissected in the laboratory.

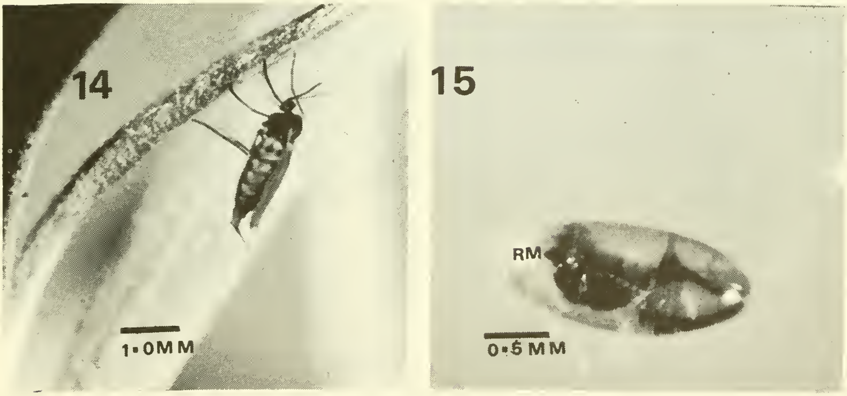
GALLS

New galls were first observed in the field on 8 July 1976 at the Blue Bell area (elevation 2,700 m) in soil with a temperature of 18° C at a depth of 7.0 cm. The aerial shoots of most of the host plants were dying by this time, but a few young secondary shoots were still active. These young galls, covered by scale leaves, occurred at the bases of the dying aerial shoots and on the young rhizomal branches. Superficially, these appeared very similar to the axillary buds.

The galls remained dormant through the fall and winter months to resume their growth the following spring. On 9 May 1977 most of the galls were already growing at Blue Bell in soil at 8° C in temperature and at a depth of 2.5 cm. The spring growth of the galls and the host plants was concommitant till the galls reached maturity by the time of pupation of the midge, beginning early in June. The adults emerged as soon as the galls began to wither and dry, by late June (Fig. 16). Some of the old galls still remained attached to the host plant even in the following year.

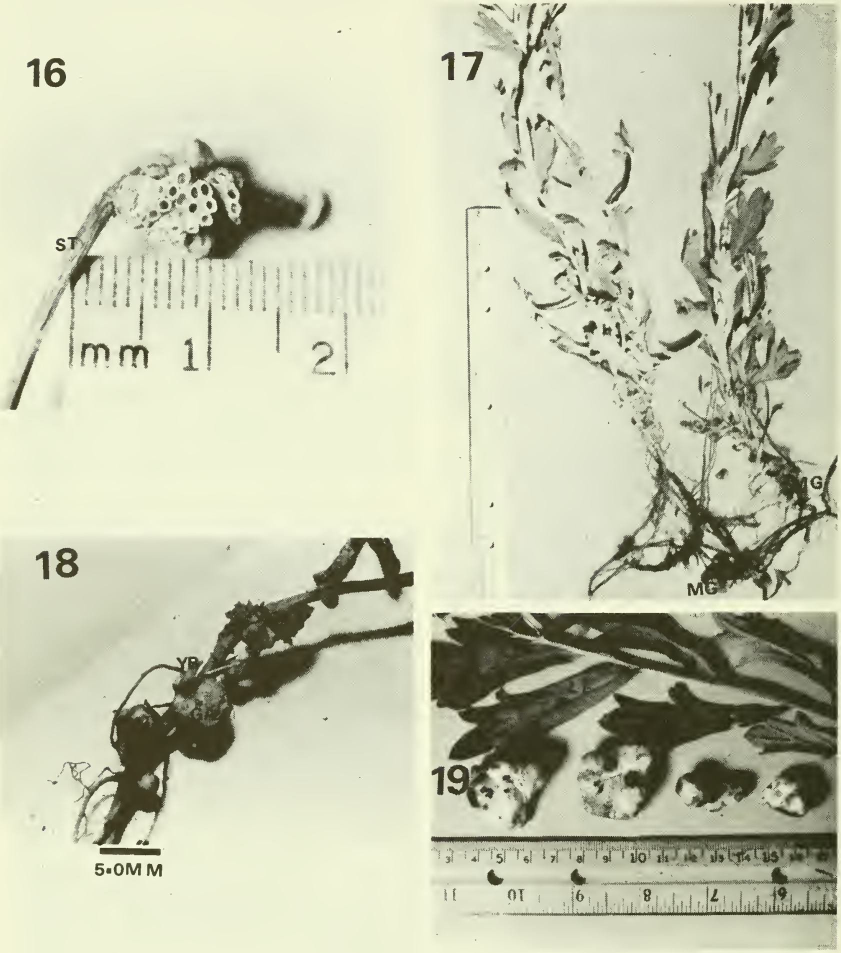
The galls were confined either to the bases of the aerial shoots (Fig. 17) or to the active young branches of the rhizome (Fig. 18). No galls were found on the lateral roots (Fig. 18) or on the old rhizome. On the shoots the galls were largely restricted to the basal subterranean areas, but a few were also found protruding just above the soil surface. The depth of the galls in soil varied, depending on the soil texture. In decaying organic matter the galls were closer to the surface than in the loose loamy soil where they were down to a depth of about 4.0 cm.

Out of a total of 77 galls examined in the laboratory, 32 (45 percent) were monothalamous and the remaining 45 (55 percent) were polythalamous. Galls occurred either singly or in clusters (Fig. 19). Single galls were more or less globose and the largest single gall measured 8.5 mm in diameter. The largest cluster of galls reached 25.0 mm across. These galls were creamy white in color, but a few had violet-colored areas on them during the early stages of growth. The galls exposed to sunlight developed a green color in the outer tissues.



Figs. 14-15: 14, Adult female resting underneath a leaf, LE-Leaf. 15, Pupa of the parasite, RM-Remnant of the midge larva.

The gall tissues initially consisted of moist, turgid cells which became dry after the maturation of the gall. In the polythalamous galls there was only one larva per larval chamber. In a given gall all the midges were in about the same stage of development. However, different galls, even those found on the same host plant simulta-



Figs. 16-19: 16, Partly dissected midge gall after the emergence of the adults, ST-Stem. 17, *Artemisia ludoviciana* plant bearing midge galls, MG-Midge galls. 18, Young rhizomal branch of *Artemisia ludoviciana* bearing galls, GA-Gall, YB-Young axillary bud. (Note absence of galls on lateral roots.) 19, Clusters of subterranean bud galls of *Rhopalomyia subhumilis* from *Artemisia ludoviciana*, LE-Close view of the host plant leaf.

neously, contained midges growing in different stages. The regression coefficient for the relationship between the size of the mature galls and the number of midges per gall is highly significant. This relationship is shown in Figure 20.

Out of the 24 galls kept individually in the plastic vials, only female adult midges emerged from seven galls, only male adults from three galls and both male and female adults emerged from two galls. From five other galls only adult parasites emerged. Both female adult midges and adult parasites emerged from two galls, and none emerged from the remaining five galls.

The attempt to induce gall formation by exposing uninfested plants to the newly emerged midges in the laboratory was not successful. However, when a number of infested host plants were allowed to grow inside a growth chamber, new galls were observed on the new shoots on 2 September 1976 and adults, possibly belonging to a second generation, were collected from these galls on 22 October 1976.

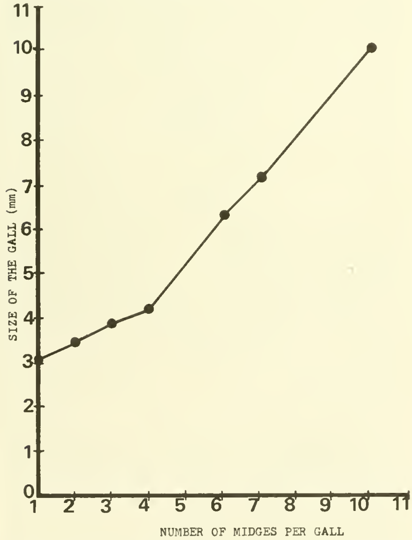


Fig. 20. Relationship between the number of midges per gall and the average size of the galls, (1976–77).

Discussion

These results indicate that the midge galls are modified axillary buds found either at the bases of the aerial shoots or on the new branches of the rhizome. Since only some of the aerial shoots and rhizomal branches had galls on them they are not likely to be the natural outgrowths of the host plants. On the contrary, the young galls and the axillary buds are so similar in appearance, it is not possible to distinguish between them without dissection under the microscope. Both the galls and the axillary buds are covered with scale leaves in the early stages of development and become activated about the same time in the spring. The spring and summer activation of the growth is characteristic of most of the other bud galls (Mani 1964). The absence of the galls either on the lateral roots or on the old rhizome, both of which are devoid of any active buds, further supports the view that these galls are modified buds. This view is also in accord with the preference of *Rhopalomyia* species for the bud galls (Felt 1915, 1940).

These growing buds may be preferred by the gall midges because they are well protected, readily supplied with the nutrients, and are in an active meristematic state—all of which are helpful for the formation of the galls (Felt 1936). Growing buds also may offer easily penetrable tissue for the young midge larvae. Subterranean buds in particular provide a microhabitat explored by relatively few other insects and apparently by none others in the case of *Artemisia*. The comparatively low rate of parasitism and apparent lack of inquilinism also indicate that subterranean galls could provide better protection for these midges.

The presence of the larvae of these midges in each and every gall dissected in the laboratory indicates that they may be the causative agents. The appearance of the galls in those buds close to the soil surface shows that they are caused by an aerial species (Mani 1964). Furthermore, the growth patterns of the galls and the midges are closely related. Although the laboratory induction of the galls by these midges was not successful, their ability to induce galls was indicated by the emergence of a possible second generation of adults in October from those infested plants grown inside a growth chamber. The failure to induce galls was partly due to the asynchrony between the emergence patterns of the limited number of the adult males and females in the cage which resulted in their deaths without mating and the decaying of some of the galls brought from the field, probably due to their continuous contact with the nutrient medium. Attempts by Spence (1969) to induce galls of *Rhopalomyia hirtipes* in the laboratory also failed.

Association of bacterial and other types of microorganisms with the galls has been reported by others (Mani 1964). But the only report of bacterial microorganisms from *Rhopalomyia* galls is that by Farnsworth and Hammond (1968) for the galls of the midges under discussion. The attempts to find either the nitrogen-fixing bacteria by electron microscopy or to confirm the nitrogenase activity from these midge galls failed (Kent, unpublished data).

The eggs of these midges are laid in the leaf axils, which apparently provides them with shelter and protection from dessication. The female ovipositor is not adapted to lay the eggs into the host plant tissues and, consequently, eggs were never observed inside the host tissues. But the laying of some eggs on the wall of the glass tubes may be an indication of laying them on other inert surfaces like soil. But this was observed under the artificial conditions in the laboratory, and the eggs of this midge were never recovered from soil in the field. The eggs are comparatively smaller than in the related species and were visible to the unaided eye only when found in clusters. In the field the eggs were found over a period of three weeks, which apparently is responsible for the overlap of the different developmental stages.

The first stage larva was mobile and presumably induced the galls by invading the axillary buds. The exact mechanism of gall formation is not known. Since these young larvae lack well-developed mouth parts it is unlikely they bored into the host plant tissues. The passage of digestive enzymes from the larva to the gall tissues has been reported for other midge larvae (Bronner 1970), and it is possible for these midge larvae to secrete enzymes which could digest the host plant tissues, enabling them to enter the axillary buds. The larva is the sole trophic stage in the life cycle since the adults were never observed to feed. None of these midge larvae contained any smaller larvae inside them anytime, unlike in the case of the paedogenetic ones. Also, the adults of both sexes emerged from the same gall, which indicated again the lack of paedogenesis. Monothalamous galls are unlikely for the paedogenetic larvae, when only one larva is present in the mature state, as was found for these midges.

Inhabitants of a given gall were at about the same stage of development, which indicated the possibility of gall initiation by several larvae simultaneously. But even one larva is capable of gall initiation, as shown by the presence of the monothalamous galls. The young, first instar larvae presumably invaded the axillary buds at random. But since the number of axillary buds suitable for gall initiation would be limited at any given time, it is possible for the larvae from the same egg cluster to attack the same axillary bud and, therefore, to be found in about the same stage of development later.

The size of a given gall was directly proportional to the number of midges found inside, which indicated a cumulative effect by the larvae which appeared to be the main influencing factor. The gall clusters may be the result either of multiple invasions by the young larvae at different intervals of time or an unusually large invasion by the young midge larvae on the same bud simultaneously.

As expected by the relatively long period of occurrence of the eggs in the field, different galls growing at the same time had larvae of different stages. The number of larval stages could not be determined, since the growing larvae did not survive outside the galls. But for most Cecidomyiidae, the number of larval stages has been reported to be three (Gagné 1968).

Pupation occurred inside the galls as in most other *Rhopalomyia* species. The protrusion of the pupal exuviae perhaps facilitated the emergence of the newly hatched adult through the soil, although this has been observed for aerial species of midges as well (Spence 1969). This need for the adult to emerge through the soil imposes another restriction on the possible depth of the gall in soil. The vigorous preemergence movements of the pupa could help the passage of the pupal case containing the adult through the gall and soil under the field conditions.

The presence of some galls with adult midges belonging to one sex could be due to chance, since the females outnumber the males 2:1. Sex induction by the environment is another possibility, but no apparent relationship between the occurrence of this phenomenon and any one of the likely external factors could be found. Jones (1971) observed a similar relationship between the adult sex and the galls for a related midge species.

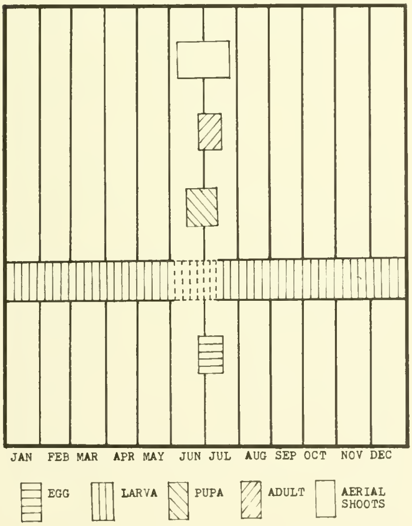


Fig. 21. Seasonal occurrence of *Rhopalomyia subhumilis* developmental stages and aerial shoots of *Artemisia ludoviciana* at Philadelphia Flat in 1976.

The short adult life span is common to most gall midges. This short life span, lack of feeding by the adults, and apparent need for mating prior to oviposition could all contribute to the need for quick oviposition and the localized pattern of infestation observed in the field. The sex ratio indicates the possibility of multiple matings for the male.

Apparently there is one generation of midges per year in the study areas since the eggs and the other developing stages were observed only in one continuous period during the year and the host plants had one relatively short growing season (Fig. 21).

Acknowledgments

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THE ALPINE BUTTERFLIES OF CASTLE PEAK, NEVADA COUNTY, CALIFORNIA

Arthur M. Shapiro[1]

Abstract.— The west slope of Basin and Castle peaks and the ridge between them displays a wind-generated tree line below 8500 ft, with dry alpine fell-field vegetation above. The butterfly fauna, although depauperate compared to that of the High Sierra farther south, includes some truly boreal elements such as *Oeneis ivallda, Plebeius shasta,* and *Hesperia nevada.* These species commonly occur 1500 to 4000 ft higher in the southern Sierra.

The Sierra Nevada of California is about 360 miles long, from the Lassen Peak area in the north to Walker Pass in the south. Along the crest the summits become progressively higher southward—from 6000-8000 ft in Plumas and Sierra counties to 10,000 ft west of Lake Tahoe, 13,000 ft in Yosemite National Park, and 14,000 ft near Mount Whitney. The term "High Sierra" is properly applied to the region from slightly north of Yosemite to Cottonwood Pass. This area, averaging 20 miles wide over its 150-mile length, includes about 90 percent of the Arctic-Alpine life zone in California. Tree line drops below 10,000 ft from Pyramid Peak northward, reaching about 9000 ft on the north side of Lassen Peak (where it is ill-defined due to the rocky substrate), but there are few areas of alpine vegetation in the northern Sierra, and they have not been well studied by biologists. The most extensive of them south of Lassen Peak is on the west side of the andesitic mass forming Basin Peak (9015 ft), Castle Peak (9103 ft), and the ridge connecting them. Castle Peak is the second highest in Nevada County and in the Sierras proper, north of Donner Pass.

The Sierran Arctic-Alpine butterfly fauna is best known around Tioga Pass (9941 ft), where fell-fields are readily accessible in a day's hike from a good road. Tilden (1958) and Garth and Tilden (1963) have reported in detail on its composition and ecological characteristics. Another fairly well-known, though unpublished, alpine fauna is that of Sonora Peak (11,429 ft), again because of its proximity to a road. Lepidopterists have visited other alpine areas including some to the north, but have not reported on their findings. Although Castle Peak (long known as Stanford Peak or Mt. Stanford) has been collected by botanists for over a century, I can find no record of its having been investigated for butterflies before 1972. This is surprising, since it is an easy day's hike from Interstate Highway 80 (formerly U.S. 40); perhaps the forbidding south face of the mountain, which gives it its name, has given it a more difficult reputation than it deserves (Fig. 1). Again, it has not been widely recognized that an alpine fell-field was present on this mountain; True (1973) states that the Arctic-Alpine life zone does not occur in Nevada County. This is a matter of interpretation, since so many organisms are distributed as if it does. The vegetation, as described below, demonstrates that the summit community is easily considered an alpine fell-field, and not even a very depauperate one. Smith (1973) notes that around Lake Tahoe "scarcely any of the lower peaks between 8500 and 9500 ft are forested at their summits and these support an illusion if not, in fact, the actual plant associations of summit screes and alpine fell-fields."

The Alpine Vegetation

Tree line is developed only on the west side and is obviously related to the prevailing westerly wind. This was noted as early as 1921 by Smiley (p. 57). No meteorological data are available for Castle Peak, but its orientation and elevation far above the surrounding terrain, the persistent pressure gradient across Donner Pass, and its location overlooking the great canyon of the South Yuba River predispose it to high winds. In my experience it is a very unusual day when the midafternoon wind on the

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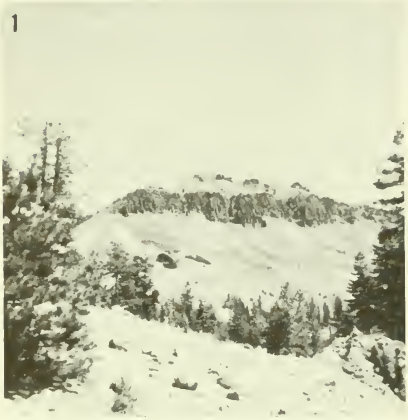

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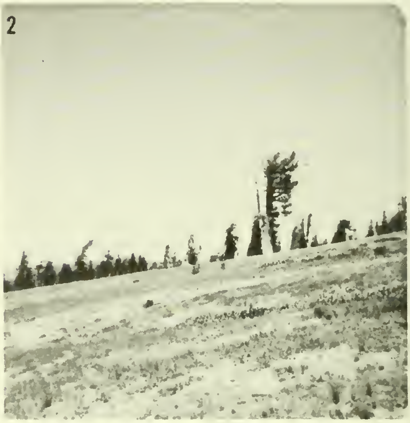

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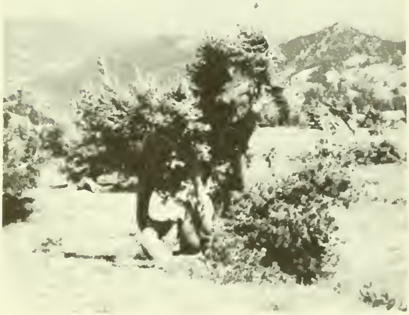

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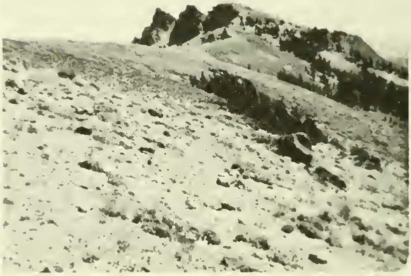

Fig. 1. Southwest face of Castle Peak seen from near Castle Pass, showing eroded "badlands" and unvegetated talus. This is the aspect of the mountain visible from the highway.

Fig. 2. Trees along the jeep trail below Basin Peak, showing shaping by prevailing westerly wind at about 8000 ft.

Fig. 3. Upper edge of subalpine forest belt, showing *krummholz* of lodgepole pine and mountain hemlock below the ridge top south of Basin Peak.

Fig. 4. Tree line is clearly visible on the west side below the ridge; note "crawling tree." Photographed from near summit of Basin Peak.

ridge top is less than 20 mph. The trees show abundant evidence of battering by the west wind (Figs. 2-4). Matted *krummholz*, consisting of *Pinus murrayana* Grev. & Balf., *P. albicaulis* Engelm., and especially *Tsuga mertensiana* (Doug.) Carr., occurs as much as 350 ft below the ridge top on the west side, and farther down the tops of the trees are commonly bent to the east. On the east side erect, pyramidal trees come almost up to the ridge top. A few nearly prostrate trees occur at low points along the ridge, and one large individual (known locally as the "crawling tree") is pressed almost flat against a 45 degree slope just below the crest.

The extensive treeless area which I am calling a fell-field (Figs. 5-8) includes about 100 species of vascular plants. Seventy of these are listed as alpine fell-field inhabitants by Munz (1970) and five are listed only from that community. Of the 24 "indicator" plants listed for alpine fell-fields by Munz (1970: 10-18), 6 occur on Basin and Castle peaks. Smiley (1921) lists some additional alpine "indicators" which occur on Basin-Castle peaks. The alpine flora includes the following distinctive taxa: *Artemisia tripartita* Rydb., *A. arbuscula* Nutt., *Railardella argentea* (Gray) Gray, *Haplopappus macronema* Gray, *Castilleja ambigua* Jones, *C. lemmonii* Gray, *Polemonium pulcherrimum* Hook., *Gentiana newberryi* Gray, *Primula suffrutescens* Gray, *Cassiope mertensiana* (Bong.) D. Don., *Epilobium obcordatum* Gray, *E. anagallidifolium* Lam., *Linum lewisii* Pursh., *Lupinus lobbii* Gray, *Astragalus whitneyi* Gray, *A. austinae* Gray, *A. bolanderi* Gray, *Ivesia gordonii* (Hook.) T. & G., *Potentilla drummondii* ssp. *Bruceae* (Rydb.) Keck, *Sibbaldia procumbens* L., *Purshia tridentata* (Pursh.) DC., *Saxifraga aprica* Greene, *S. bryophora* Gray, *Draba crassifolia* Grah., *D. densifolia* Nutt., *Erysimum perenne* (Wats.) Abr., *Ranunculus eschscholtzii* var. *oxynotus* (Gray) Jeps., *Silene sargentii* Wats., *Lewisia pygmaea* (Gray) Rob., *Oxyria digyna* (L.) Hill, *Eriogonum ovalifolium* var. *nivale* (Canby) Jones, *Salix anglorum* var. *antiplasti* Schneid., *Carex helleri* Mkze., etc. In Table 1 the 232 species of vascular plants collected by True (1973) and myself have been categorized by the plant communities in which they are recorded by Munz (1970). The boreal character of the vegetation emerges clearly from these statistics. Although only 18 plant species are shown as being of east-slope distribution, the Castle Peak alpine fell-field (like many in the High Sierra) shows a marked east-slope aspect, accentuated by the conspicuousness of *Artemisia* and *Purshia*. Much of the alpine flora of the Sierra is believed to be evolutionarily derived from the high desert (Chabot and Billings 1972). After snowmelt the thin, porous alpine soil dries out rapidly; occasional air-mass thunderstorms in summer temporarily replenish surface moisture. Such thunderstorms are rather more frequent on Castle Peak than in the surrounding area, presumably because its greater elevation promotes the growth of cumulus.

I have collected the Basin-Castle peaks area 13 times from 1972 through 1977. The entire area above tree line was collected on two dates: 28 July 1976 and 8 July 1977. The general Donner Pass region has been visited over 100 times since 1972.

THE BUTTERFLY FAUNA

Family Satyridae

Oeneis ivallda (Mead).— The most characteristic Sierran alpine butterfly, *ivallda* occurs from about 7000 ft in the east end of Donner Pass (presumably as a stray) to 14,000 ft in the southern Sierra. Breeding

TABLE 1. Occurrence of the 232 plant species recorded from Basin-Castle peaks by plant communities recognized in the Sierra Nevada by Munz (1970). The mean number of categories (not communities) per species is 2.65.

Community	**Number of Species**
Sagebrush scrub (east slope)	18
Yellow pine forest	95
Red fir forest	138
Lodgepole pine forest	149
Subalpine forest	123
Alpine fell-field	70
Many communities (widespread)	22

colonies exist about 8000 ft on Mt. Judah and Anderson Peak in Donner Pass south of Interstate 80, but the one on Basin-Castle is the only colony known north of that road. There may be a colony on the smaller alpine summit of Mt. Lola (9143 ft) a few miles to the north. *Oeneis ivallda* was extremely abundant all along the crest on 8 July 1977, with 250 to 300 individuals seen. It was most numerous in the alpine sage-

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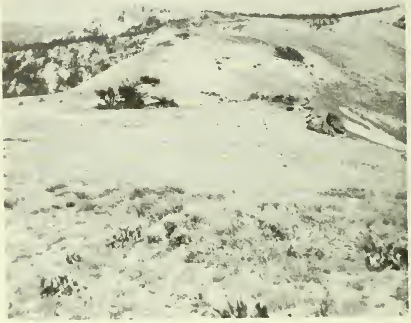

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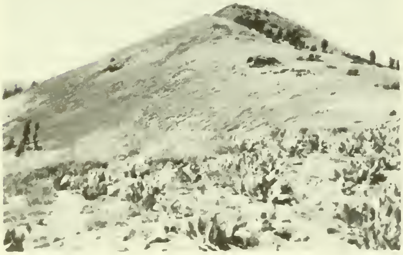

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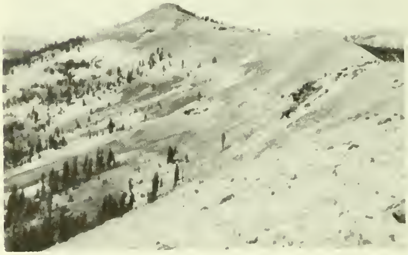

Fig. 5. Habitat of *Oeneis ivallda* just below summit of Basin Peak; turf of sedges, grasses, *Eriogonum* species, and *Astragalus whitneyi*.

Fig. 6. Habitat of *Oeneis ivallda* and *Hesperia nevada* in alpine sagebrush, grasses, and composites below Basin Peak.

Fig. 7. Ridge top showing trees on east side and alpine vegetation on west. Large-leaved plant in foreground is *Wyethia mollis* (Compositae).

Fig. 8. Ridge top looking northwest from Castle Peak, showing extent of area above tree line.

brush areas and around isolated rock outcrops. It is said to have a two-year life cycle and to be absent in many colonies in even-numbered years, but it was taken on Castle Peak in 1976. Variation is marked, especially in males. The host plant is unknown; 49 species of grasses and sedges are known from its habitat here.

Cercyonis oetus (Boisduval).— An east-slope element, this small brown Satyrid is common long after *Oe. ivallda* in the same places, flying mostly in August and on into early September after most other species have disappeared. It is presumably a grass feeder.

Family Nymphalidae

Speyeria egleis (Behr).— Males are abundant hilltoppers along the crest in July and August, but no females have been collected. This is the only silver-spotted fritillary seen in the alpine fell-fields, which are too dry for *S. mormonia arge* (Strecker).

Phyciodes campestris montana Behr.— Occasional, June to August, but not known to breed. Much more common on dry or moist slopes in the lower subalpine areas.

Polygonia zephyrus (Edwards).— Infrequent; worn specimens of both sexes (hibernators) on the crest in July. Breeding status unknown. This is a very common, widespread species around Donner Pass.

Nymphalis californica (Bdv.).— Occasional, especially in migration years. There are no *Ceanothus* (Rhamnaceae) on the ridge top, but several species used by this insect occur in subalpine areas below.

Nymphalis milberti (Godart).— Three seen (one taken) on the ridge top, apparently hilltopping, 8 July 1977. The host plants (*Urtica* spp.) do not occur above tree line. A female found on Basin Peak, 9 August 1977.

Vanessa virginiensis (Drury).— Occasional, July to September. Three potential host plants are recorded, but no larvae have been found.

Vanessa annabella (Field).— Occasional, July to August. A female was taken on 8 July 1977, and the usual host plant at Soda Springs, *Sidalcea glaucescens* Greene (Malvaceae), occurs on Basin Peak.

Family Lycaenidae

Satyrium fuliginosum (Edwards).— Common all along the ridge top, second half of July. The butterflies scarcely fly at all unless disturbed, and they may be seen walking on *Eriogonum* and yellow composite flowers on windy afternoons. Four species of lupines occur on the summit, but I have been unable to establish an association.

Callophrys lemberti Tilden.— Frequent, mid-June to mid-July, among *Eriogonum* plants and, like the last species, seldom seen flying. The host is presumably an *Eriogonum;* eight taxa are recorded here.

Lycaena nivalis (Bdv.).— Occasional on the ridge top among the *Eriogonum* or on composites, but less common than in the subalpine areas along the trail to Castle Pass. Late June to early August.

Lycaena heteronea Bdv.— Frequent in "rock gardens," second half of July, presumably feeding on an *Eriogonum.* Females are quite dusky.

Everes amyntula (Bdv.).— In the northern Sierra and the Trinity Alps occurs a subalpine-alpine *amyntula* which is larger and duller than the montane coniferous forest populations associated with native *Vicia* and *Lathyrus* at 1000 to 5000 ft. This animal, which occurs at 7500 ft in Trinity County and above 8500 ft in the Donner Pass area (Mt. Judah, Anderson Peak, Basin-Castle) is associated with *Astragalus whitneyi* Gray (Leguminosae) and oviposits in the inflorescences. Like other lycaenids on Castle Peak, these animals seldom fly and may have to be scared up from the plants. They occasionally visit flowering *Eriogonum. Everes amyntula* is done flying before *Plebeius shasta* (Edw.) begins flying in the same places; its peak flight is in early July.

Philotes enoptes (Bdv.).— A single aberrant male was taken on 8 July 1977 along the ridge top. It was not associated with an *Eriogonum.* This species is so sedentary that a breeding colony must be assumed to exist.

Celastrina argiolus echo (Edw.).— Occa-

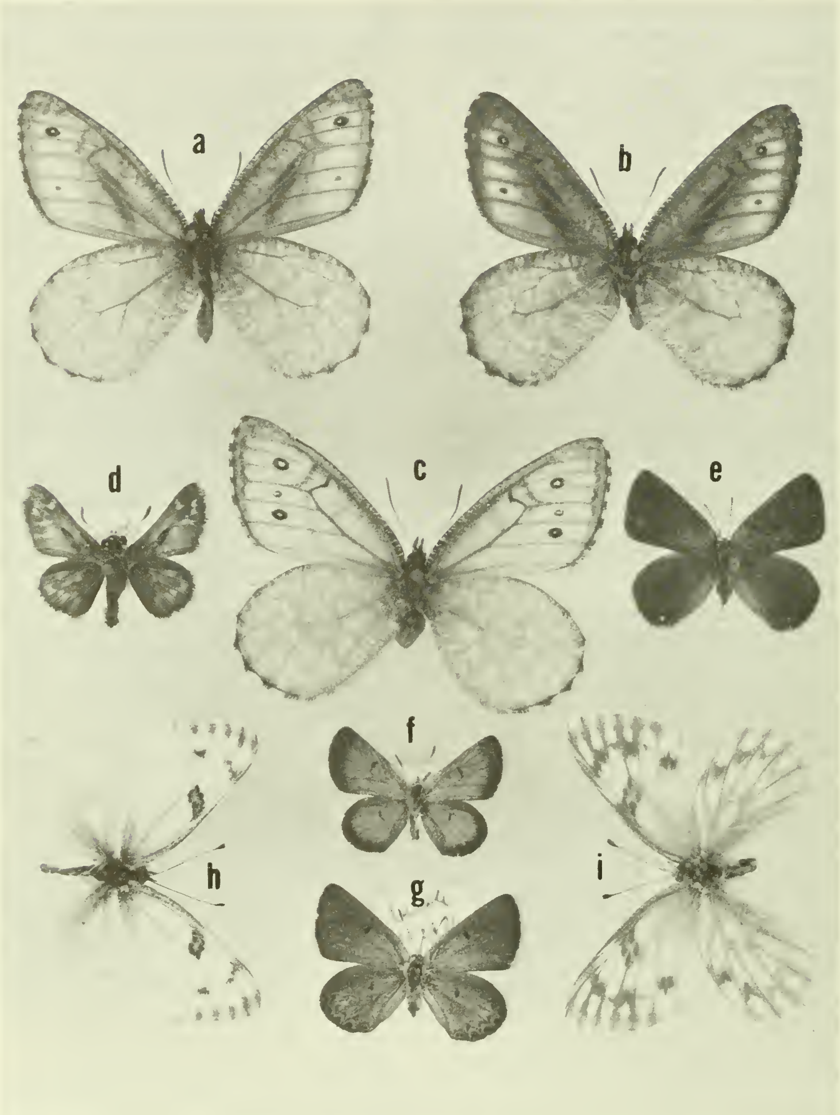

Fig. 9. Characteristic alpine butterflies from Castle Peak area: a, b, light and dark male *Oeneis ivallda;* c, female *Oe. ivallda;* d, male *Hesperia nevada;* e, female *Satyrium fuliginosum;* f, g, *Plebeius shasta* male and female; h, i, *Pieris occidentalis* male and female.

sional, June to mid-July, both sexes. Breeding status uncertain. Much commoner in the subalpine zone lower on the mountain, where its hosts (especially *Ceanothus*) are common.

Plebeius saepiolus Bdv.— Occasional, July. Two clovers (*Trifolium monanthum* Gray, *T. productum* Greene) occur on Castle Peak. This is one of the most common species in the meadow at Castle Valley.

Plebeius icarioides (Bdv.).— Common throughout July. On the ridge associated with *Lupinus arbustus* Dough. ssp. *silvicola* (Hell.) D. Dunn.

Plebeius shasta (Edw.).— Like *Oeneis ivallda*, this is a characteristic Sierran alpine butterfly. It is incredibly abundant from mid-July through mid-August, and very variable, although consistently larger than material from Inyo and Mono counties. It oviposits on pedicels of *Astragalus whitneyi* Gray, often on the same plants on which *E. amyntula* laid three weeks before.

Plebeius acmon (Westw. & Hew.).— This ubiquitous, weedy species occurs as a stray and may breed occasionally, but does not overwinter. Recorded from July to September.

Plebeius lupini (Bdv.).— Common in "rock gardens," where it is associated with *Eriogonum umbellatum* var. *covillei* (Small) Munz & Reveal, which is also the host plant in Donner Pass. Late June to mid-July.

Glaucopsyche lygdamus behrii (Edw.).— Resident but not common, late June to early July. Associated with *Lupinus polyphyllus* Lindl. ssp. *superbus* (Hell.) Munz. in a seep area on Basin Peak.

Family Pieridae

Colias eurytheme Bdv.— A common flyup, perhaps breeding but never overwintering; all season.

Pieris sisymbrii Bdv.— Frequent, late June to mid-July. Males hilltopping; females not seen, and breeding status uncertain; females have been collected in Donner Pass.

Pieris occidentalis Reakirt.— The most common butterfly on the ridge top, flying mid-June to September. Males hilltop, but females are not uncommon. Very variable. Eggs and larvae have been collected on the following Cruciferae: *Arabis holboelli* Horn. vars. *pinetorum* (Tids.) Roll. and *retrofracta* (Grah.) Rydb., *A. platysperma* Gray, *Descurainia richardsonii* ssp. *viscosa* (Rydb.) Detl., and *Draba crassifolia* Grah. This is the only resident butterfly on Castle Peak that may be partially double-brooded (some years). (Note: *P. protodice* Bdv. & LeC. has not been seen on Castle Peak but was recorded in the subalpine zone in 1972 and again in 1977.)

Anthocaris sara stella Edwards.— Occasional as a hilltopper, males only seen; breeding status uncertain. Here, as in Donner Pass (Emmel and Emmel 1962, Shapiro, unpublished), occasional white males indistinguishable from *A. s. sara* Lucas are found. Eastward and lower, at Truckee, only the yellow form occurs. This situation deserves further attention.

Euchloe ausonides Lucas.— One male, 8 July 1977 on the ridge top. This small race of *ausonides* is about the same size as the next species, flies with and a bit after it, and is commonly confused with it. I have it from the Trinity Alps to Eldorado County, 5000 to 9000 ft. It may be recognized by the thinner bar at the end of the forewing cell; somewhat duller white color; less intense green mottling below; and more angular hindwing. It seems always to be rare.

Euchloe hyantis (Edw.).— A common hilltopper, mid-June to mid-July. It is not uncommon to find *hyantis*, *sisymbrii*, and *occidentalis* flying together around the same rocky crag on Castle Peak.

Family Papilionidae

Papilio zelicaon Lucas.— Common. Males hilltop, and females are occasionally encountered (especially on the ridge from Castle Pass to Castle Peak). Late June to early August. Host plant unknown; presumably one or more of the six recorded Umbellifers.

Papilio indra Reakirt.— Frequent. Males hilltop, and females are occasionally seen on the crest and also on the ridge to Castle

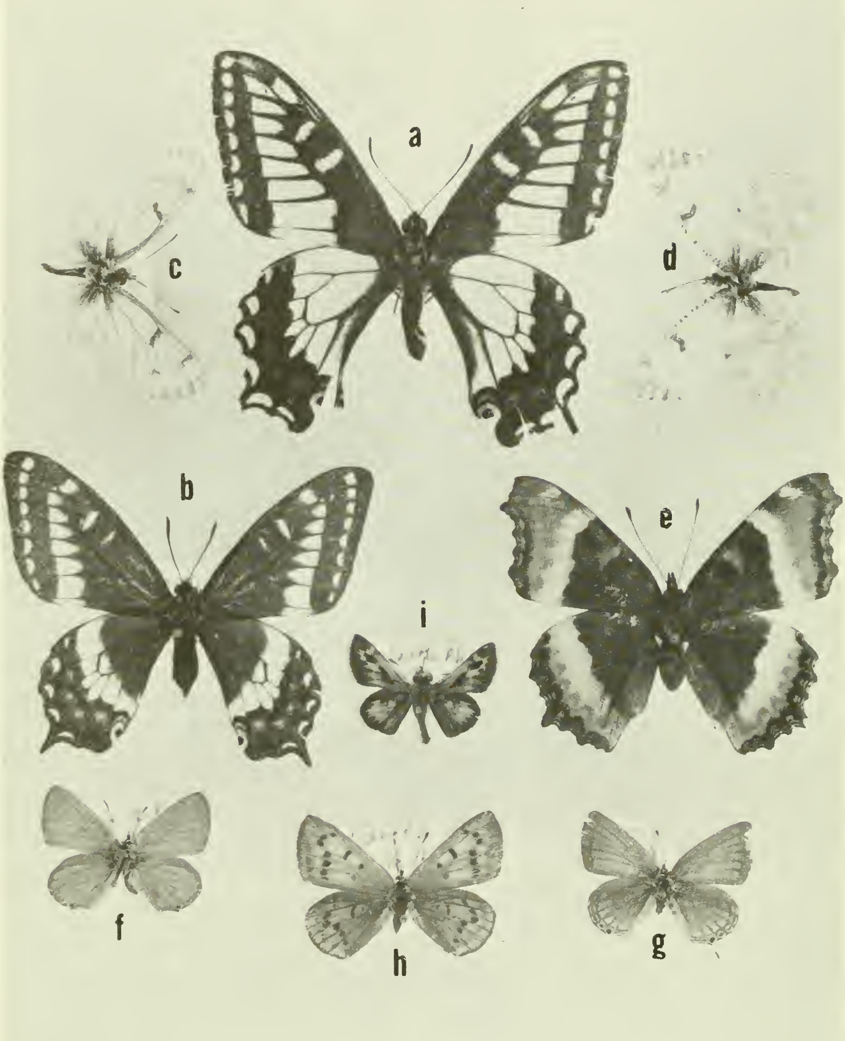

Fig. 10. Characteristic alpine butterflies from Castle Peak area: a, male *Papilio zelicaon;* b, female *Papilio indra;* c, male *Pieris sisymbrii;* d, male *Euchloe ausonides;* e, female *Nymphalis milberti;* f, g, *Everes amyntula* male and female; h, female *Lycaena heteronea;* i, male *Polites sabuleti tecumseh.*

Pass. Late June to mid-July. Oviposition observed on *Lomatium dissectum* var. *multifidum* (Nutt.) Math. & Const.

Papilio eurymedon Lucas.— Occasional male hilltopper, July; the host plants do not occur above tree line.

Parnassius clodius baldur Edwards.— Occasional, both sexes, July, probably flyups from the subalpine area where it is quite common.

Family Hesperiidae

Hesperia juba (Scudder).— Occasional, June and September; breeding status unknown. A very widespread species around Donner Pass.

Hesperia harpalus yosemite Leussler.— Only male hilltoppers thus far recorded, second half of July, occasional.

Hesperia nevada (Scudder).— Occasional on the ridge top and crags, both sexes, first half of July. This very dark, small, shaggy skipper is a true alpine species in the Donner Pass region. The Emmels (1962) found it on the summit of Mt. Judah (8243 ft).

Polites sabuleti tecumseh (Grinnell).— Infrequent, grassy area below ridge top, first half of July. Much more common in the subalpine meadows, where it oviposits on *Agrostis scabra* Willd. and perhaps other grasses.

Pyrgus communis (Grote).— Common, first half of July, ovipositing on *Sidalcea glaucescens* Greene (Malvaceae).

Pyrgus ruralis (Bdv.).— Infrequent; grassy open places on the ridge mid-June to early July. Host plant unknown.

Erynnis propertius (Scud. & Burg.).— Occasional hilltopper, males only. July. Common in subalpine areas.

Thorybes nevada Scudder.— Occasional on the ridge as a hilltopper, probably not breeding; late June to mid-July. Abundant in Round and Castle valleys.

COMPARISONS TO TIOGA PASS

Tilden's Tioga Pass study area is much more ecologically diverse than Basin-Castle Peak. It includes a spread of over 3000 ft in elevation, moraines, boggy areas, and wet meadows above tree line. He records 43 species, as against 40 in the present study; 5 are alpine obligates, as against 3 at Castle Peak. Missing at Castle Peak are the alpine species *Chlosyne damoetas malcolmi* (Comstock), *Colias behrii* (Edwards), and *Hesperia miriamae* MacNeill. All of these are High Sierran endemics unrecorded north of Yosemite.

Some species found at Tioga Pass above tree line are strictly subalpine species farther north around Donner Pass. These include *Speyeria mormonia arge* (Strecker), *Lycaena editha* (Mead), *L. mariposa* Reakirt, *L. cupreus* (Edwards), and *Agriades glandon podarce* (Felder and Felder). One species, *Lycaena rubidus* (Behr), is a common member of the alpine fauna at Sonora Peak, occurs in Donner Pass, and may yet turn up at Castle Peak where at least one of its known hosts, *Oxyria digyna* (L.) Hill (Polygonaceae), occurs (see Johnson and Balogh, 1977). It is basically an east-slope animal. Another species found on Sonora Peak but unrecorded at either Tioga Pass or Castle Peak is the "alpine" member of the *Plebeius melissa* (Edwards) complex. At Sonora Peak and also on Gumboot Butte, far to the north in the Trinity Divide, it occurs on *Astragalus whitneyi* Gray, which is one of the most common plants on the Basin-Castle ridge top. Farther northwest, on Packer's Peak in the Trinity Alps, it is replaced on this plant by an ecotype of *P. argyrognomon anna* (Edwards), but in the Donner Pass region this insect occurs in subalpine marshy habitats on *Lupinus polyphyllus* Lindl. and has never been found at Castle Peak or on *Astragalus*. *Plebeius melissa* is predominantly an east-slope species. Multivoltine "Great Basin" *melissa* has been found in Donner Pass (Shapiro, unpublished). Another east-slope species, *Satyrium behrii* (Edw.), which occurs at Truckee and Donner Pass, has not been found on Basin-Castle although its host, *Purshia*, is common there; it is not usually an alpine butterfly in the northern Sierra.

The Donner Pass fauna as a whole is about 70 to 75 percent univoltine. Tilden claims that of the resident (as against colonizing, nonwintering) fauna of Tioga Pass only *Polites sabuleti tecumseh* is bivoltine, but this claim is spurious (see Shapiro 1975). At Castle Peak one breeding resident (*Pieris occidentalis*) and one whose status is unknown (*Hesperia juba*) appear bivoltine. Both are probably bivoltine at least in the subalpine zone at Tioga Pass as well. Of the remaining 38 species at Castle Peak, about two-thirds are "early" season emergents (e.g., *Oeneis ivallda*, *Everes amyntula*, *Hesperia nevada*), appearing about three to five weeks after bare ground appears. The remaining third are "late" (*Plebeius shasta*, *Lycaena heteronea*, *Cercyonis oetus*). In the case of *E. amyntula* and *P. shasta*, which have the same host plant, this seasonal difference may facilitate coexistence. The flight season in a "normal" year is about 100 days, from late June to late September. Only one species, *Pieris occidentalis*, a famous hilltopper, covers most of that period.

One alpine species found elsewhere in the Donner Pass vicinity (*Parnassius phoebus behrii* Edw.) has not been found on Basin-Castle Peak, apparently because its host, *Sedum obtusatum* Gray, is extremely rare on the andesite substrate. It is common on granite, and the butterfly is thus effectively edaphically restricted. It ranges north to Plumas County, where it occurs at considerably lower elevations.

The isolated character of alpine "islands" in the northern and north-central Sierra makes them ideal subjects for biogeographic analysis. As Lepidopterists become less automobile-bound, increasing amounts of data may become available which will help in the eventual formulation of a biogeographic synthesis of the sources of our high-elevation fauna. In the meantime, the elevational and associational flexibility of so many Sierran butterflies underscores the applicability of the "individualistic" approach to their distributions, rather than a rigidly "zonal" approach such as is commonly found in the butterfly literature.

Acknowledgments

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GEOGRAPHIC VARIATION IN *CONTOPUS SORDIDULUS* AND *C. VIRENS* NORTH OF MEXICO

M. Ralph Browning[1]

Abstract.— Geographic variation in plumage color between populations of *Contopus sordidulus* is minor. The differences in color between the races described by Burleigh (1960) is largely the result of postmortem color changes of museum skins. Variation in wing chord and length of tail between samples does not support recognizing additional races of *C. sordidulus*. *Contopus virens* is monotypic. The relationships between *sordidulus* and *virens* is unclear.

In a review of *Contopus sordidulus* (Western Wood Pewee) Burleigh (1960) proposed four nomenclatural subdivisions for the populations of the species north of Mexico. He recognized *saturatus* Bishop, 1900, and subdivided *veliei* Coues, 1866, into three races, *veliei* and two new races, *amplus* and *siccicola*. This subdivision was considered untenable by Mayr and Short (1970), who suggested that the only valid race north of Mexico is *veliei*. The AOU (1957) Check-list recognized both *veliei* and *saturatus* as races of the northern populations of *C. sordidulus*.

To determine the extent of geographic variation in the northern populations of *C. sordidulus* I compared Burleigh's type series of *amplus* and *siccicola* and other specimens for variation in color and size. Specimens used in this study include those collected in June. Although birds collected at this time and earlier could be migrants, those collected later are usually too badly worn to permit meaningful color comparisons (Phillips and Parkes 1955, Phillips et al. 1966: 169, pers. observ.). All measurements (Table 1) are in millimeters.

NOMENCLATURAL HISTORY OF CONTROPUS SORDIDULUS VELIEI AND C. S. SATURATUS

Coues (1866) indicated that two color types were among his series from the southwestern United States and that Baird believed these to represent two species. Although Coues was not so convinced, he nevertheless introduced the name *Contopus veliei* for the southwestern form and gave a diagnosis to distinguish it from *C. richardsonii*, as *C. sordidulus* was then known (see Phillips and Parkes 1955). The name *veliei* as currently used is the equivalent of *C. r. richardsonii* of older usage. Parenthetically, Burleigh (1960) is incorrect in stating that Phillips and Parkes had overlooked Coues' lectotype of *veliei*. As pointed out by Phillips and Parkes (1955) and Parkes (*in litt.*, 1976), the only locality in Coues' original description is Colorado, from whence Velie sent the first example. The *ex post facto* selection of a lectotype has no bearing on the fact that Coues had already stated that the first example came from Colorado. Thus, the specimen from Fort Whipple, Arizona (chosen by Coues at Richmond's prompting), considered by Deignan (1961) as the lectotype of *veliei*, cannot be regarded as a primary type. The type locality of *veliei* is the mountains of Colorado as stated by Phillips and Parkes (1955). The change in the type locality of *veliei* has no nomenclatural effects.

Contopus sordidulus veliei was recognized by Phillips and Parkes (1955) and the AOU (1957) Checklist as the race breeding from central eastern Alaska south through southern Mackenzie, northeastern Alberta, northwestern and central Saskatchewan, and central Manitoba, the eastern parts of North and South Dakota to central and western Texas. The AOU Checklist gives the western boundry of *veliei* as from Alaska south through eastern British Columbia to northern Mexico. This agrees with Webster (1957), who considered *placens* van Rossem, 1940, type locality in Arizona, a synonym of *veliei.*

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The second northern race, *Contopus sordidulus saturatus,* was described by Bishop (1900) as darker dorsally than the other forms of the species. Bishop considered *saturatus* to be the race breeding from the Yukon Valley in Alaska south along the coast ranges to British Columbia. Ridgway (1907) did not recognize *saturatus* because dark birds occurred outside the range ascribed to *saturatus,* that is, within the breeding range of what is currently known as *veliei.* Although recognized by van Rossem (1945), *saturatus* was not generally accepted as a distinct race until subsequent studies by Aldrich (*in* Jewett et al. 1953) and Phillips and Parkes (1955). The breeding range of *saturatus* in the AOU (1957) Checklist is given as southwestern Alaska south through western British Columbia and west from the Cascade Mountains in Washington and Oregon.

VARIATION IN COLOR

Burleigh (1960) subdivided *veliei* into three races on the basis of size (see below) and color. In so doing he restricted the range of *veliei* to northern California, Nevada, Utah, and Colorado south through Arizona, New Mexico, western Texas, northern Baja California, eastern Sonora, and northern Chihuahua. He claimed that the two new races breed north of this region. *Contopus s. siccicola* was said to breed from southern British Columbia east of the coast ranges, and east of the Cascades in Washington and Oregon to western Montana west of the Rocky Mountains. The second new race, *amplus,* was said to breed from central Alaska, southern Mackenzie, Saskatchewan, and southern Manitoba south through British Columbia, northeastern and eastern Montana to Wyoming, and in western North and South Dakota. *Contopus s. siccicola* was described by Burleigh as the palest of the four northern forms. The upper parts in *siccicola* were said to be washed with gray, whereas Burleigh considered *amplus* to be browner, and his *veliei* to be fuscous-olive. The underparts of *siccicola* were also said to be more gray and the bel-

TABLE 1. Measurements of adult males of *Contopus sordidulus* and *C. virens.*

		Wing Chord				Tail			
	n	range	mean	S.D.	C.V.	range	mean	S.D.	C.V.
saturatus	11	83.4-88.1	86.11	1.53	1.78	62.4-67.8	64.89	1.71	2.64
California[1]	20	82.4-89.6	85.63	1.87	2.18	61.6-69.7	64.77	2.18	3.37
siccicola	12	83.3-89.0	86.97	1.65	1.90	64.6-69.7	66.28	1.58	2.38
Nevada	8	85.0-88.7	86.60	1.51	1.74	65.0-70.0	66.70	1.59	2.38
Arizona	18	85.2-88.8	86.82	1.21	1.39	63.4-68.9	65.92	1.52	2.31
amplus[2]	14	83.6-90.6	87.69	2.22	2.53	62.6-71.1	67.09	2.82	4.20
northwestern *C. virens*[3]	15	82.0-88.3	85.17	2.28	2.68	63.5-71.8	68.20	2.39	3.50
eastern *C. virens*[4]	14	82.0-88.5	84.59	1.76	2.08	63.9-70.6	66.95	2.16	3.23

[1] Specimens from south of latitude 40 degrees
[2] Montana and Wyoming
[3] North and South Dakota, Minnesota, Wisconsin
[4] East of Appalachian Mountains

ly more white (less yellow) than in *veliei* and *amplus*. Burleigh described *amplus* as differing from both *siccicola* and *veliei* by being darker and "distinctly" more brown and less olivaceous dorsally, and differing from his *veliei* by being paler and less yellow ventrally.

Burleigh probably believed *siccicola* to be paler and grayer than the other forms of *C. sordidulus* for the reasons mentioned in Mayr and Short (1970)—the museum ages of the type series of *amplus* and *siccicola* and the comparative series of his *veliei* are not similar (cf. Burleigh 1960: 143–146). The two dark races, *amplus* and *veliei*, were collected, on the average, 25 years earlier than birds assigned by Burleigh to the paler series of *siccicola*. The most recently collected specimens in Burleigh's series were collected in the 1950s with only 7 percent of these specimens assigned to *veliei* and 11 percent assigned to *amplus*, whereas 44 percent of the specimens assigned to *siccicola* were collected after 1950. As would be expected, because of the nature of postmortem color changes, the darker and browner specimens were collected much earlier than the cleaner and paler specimens.

Comparison of the type series of *amplus* with similarly old specimens of *veliei* used by Burleigh does not reveal sufficient differences in coloration to justify subspecific separation. Comparison of the more recently collected specimens making up the type series of *siccicola* with the series of *amplus* and *veliei* used by Burleigh reveals *amplus* to be, on the average, slightly paler. Using specimens of *C. sordidulus* of similar museum age from the ranges of the three named races, however, reveals that the differences in palor between *siccicola* and *veliei* and *amplus* is the result of postmortem color changes. Specimens representing the three forms cannot be separated on the basis of dorsal coloration.

I found that the underparts of *siccicola* are not noticeably paler than the other forms of *Contopus sordidulus* (*contra* Burleigh 1960). Variation in ventral coloration in *C. sordidulus* appears to be clinal from west to east, with the coastal form, *saturatus*, being slightly darker and more yellow. The paleness increases gradually eastward toward the Rocky Mountains. Specimens from the northwestern slope of the northern Rocky Mountains, however, are slightly darker. Nonetheless, ventral coloration has not proven to be useful for distinguishing between the northern forms of *C. sordidulus*.

In a recent study of the races of migrant *C. sordidulus* in Utah Behle (1967) considered *siccicola* and *amplus* as valid races. Behle followed Burleigh's suggestion that some individuals of southern populations begin nesting while other populations are still en route to more northern localities. This was a reasonable assumption based on his limited sample and is a convenient means of disposing of the considerable amount of individual variation in dorsal coloration. For example, I found that slightly pale gray birds and darker examples occur in adjacent areas in June. Although some individuals of *C. sordidulus* may be migrating north as late as June, the lack of consistent geographic variation in color among Burleigh's forms of the species argues against recognition of additional races.

The relationships of *Contopus sordidulus* populations to those of *Contopus virens* (Eastern Wood Pewee), a monotypic species of eastern North America, not mentioned by Burleigh (1960), were also examined. These two species are morphologically similar. Phillips et al. (1966) have pointed out that adult *virens* are typically olivaceous and that *sordidulus* is slightly darker and browner in plumage coloration and usually has a darker lower mandible. I compared specimens of *sordidulus* collected in eastern Montana and Wyoming with a series of *virens* from eastern North Dakota and Wisconsin. The two series may be readily separated by the browner upper parts of *sordidulus*. However, both series are consistently olivaceous above. Specimens of *C. sordidulus* from west and south of Montana and Wyoming are not as olivaceous as specimens of *C. virens* and *C. sordidulus* from eastern Montana and Wyoming.

Variation in Mensural Characters

Measurements of wing chord and length of tail of adult male *Contopus sordidulus* and *C. virens* (Table 1) show considerable overlap in these characters with nearly identical means for the geographical samples. Burleigh's (1960) characterization of *amplus* as longer-tailed than other forms of *C. sordidulus* is not upheld.

Conclusions

Geographic variation in *Contopus sordidulus* north of Mexico is slight. The amount of variation in color and size is shown to be insufficient for recognizing *amplus* and *siccicola*. These names, along with *placens*, should be considered synonyms of *C. sordidulus veliei*. The form *saturatus* should be recognized, although it is a weakly marked race. There is no pronounced geographic variation in *C. virens*.

Overlap in coloration between the northwestern samples of *C. virens* and representatives of *C. sordidulus* from eastern Montana and Wyoming suggest a close relationship between the two species. The breeding ranges of these species overlap in western Manitoba, Nebraska (Phillips et al. 1966), and in Kansas (Barlow and Rising 1965). Van Rossem (1940, 1945), Rand (1948), Aldrich (in Jewett et al. 1953), and Meyer de Schauensee (1966) have considered *virens* and *sordidulus* conspecific. Evidence of interbreeding is inconclusive, but hybridization is mentioned by Mayr and Short (1970) as occurring in the Great Plains. It is premature at this time to consider *virens* and *sordidulus* as conspecific. Field studies, urged by Phillips and Parkes (1955), where the two species come in contact, are still needed. Such studies should be conducted on territorial individuals in late May and June, during which time birds are retaining plumage suitable for color comparisons (A. R. Phillips, *in litt.*).

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DISTRIBUTIONAL PATTERNS OF MAMMALS IN UTAH

David M. Armstrong[1]

Abstract.— Based on a synthesis of recent work on distribution of mammals in Utah, the hierarchy of ecogeographic distributional units proposed by Durrant (1952) is reevaluated by numerical methods. Areographic faunal elements, distinguished on the basis of shapes of distributional ranges in North America, are identified. Relationships are shown between ecogeographic faunal units and areographic faunal elements, and their historical implications are discussed.

Biogeography seeks to describe patterns in the landscape and to understand their evolution. Utah provides a study area of considerable interest to the zoogeographer interested in faunal movements and effects of corridors, barriers, and isolation. The state is large (nearly 85,000 sq mi or 220,000 km^2) and includes a wide range of ecological conditions, from hot desert to alpine tundra. Mean elevation is roughly 6100 ft (1860 m) and the range of relief is from about 2000 ft (610 m where Beaverdam Wash leaves the state in the southwest) to nearly 13,500 ft (4115 m at the summit of Kings Peak in the Uinta Mountains). A north-south "archipelago" of mountains and high plateaus divides Utah roughly in half. The eastern part is drained by the Colorado River and its tributaries, which have carved horizontal sedimentary formations into an intricate landscape of basins and canyons. West of the central highlands lies the Great Basin, a complex area of minor mountain ranges and internal drainage, dominated by the vast bed of Pleistocene Lake Bonneville.

The only previous zoogeographic analysis of mammals of Utah is that of Durrant (1952), who distinguished "faunal areas" in the state. These were ecogeographic units, roughly comparable to the biotic provinces of Dice (1943). Faunal areas were recognized subjectively, by the coincidence between mammalian distributions and physiographic units. Durrant (1952: 480) pointed out that faunal areas tended to be centers of differentiation for subspecies. Kelson (1951) discussed the influence of the Colorado River and its major tributaries on differentiation and distribution of rodents, refining Durrant's work on faunal areas. Marshall (1940) studied ecological biogeography of mammals on islands in the Great Salt Lake. Lee (1960) investigated the montane mammals of several mountain ranges in southeastern Utah in an effort to understand faunal relationships among the highland faunas and the effects of Pleistocene climatic change on the patterns observed. Brown (1971, in press) studied montane mammals of Utah as an example of insular biogeography. Armstrong (1973) discussed zoogeographic relationships of mammals in Canyonlands National Park, which lies astride the confluence of the Colorado and Green rivers. This work in southeastern Utah suggested some intriguing local patterns of ecological and historical biogeography, but the existing literature was inadequate to place the area in a broader context. The present paper is meant as a partial answer to this need. Its purpose is to refine ecogeographic analyses of previous authors and to provide an areographic analysis of the mammals of Utah.

Methods

Analyses of range limits in Utah were based on maps of 92 species. Seventeen species range essentially statewide in suitable habitat and hence were not mapped: *Myotis lucifugus, Myotis volans, Myotis evotis, Myotis leibii, Lasionycteris noctovagans, Eptesicus fuscus, Lasiurus cinereus, Plecotus townsendii, Peromyscus maniculatus, Erethizon dorsatum, Canis latrans, Bassariscus astutus, Mustela frenata, Taxidea taxus, Mephitis mephitis, Spilogale putorius*, and *Lynx rufus*. (These species are included in analyses of faunal areas.) Twelve species are known from too few localities to allow their ranges in Utah to be outlined with any confidence: *Sorex merriami, Sorex nanus, Notiosorex crawfordi, Myotis velifer, Euderma maculatum, Idionycteris phyllotis, Tadarida macrotis, Ondatra zibethicus, Procyon lotor, Martes pennanti, Lutra canadensis, Odocoileus virginianus*. Three species (*Canis lupus, Ursus arctos*, and *Bison bison*) have been extirpated in Utah over the last 125 years; limits of their former ranges are unknown. In addition, the natural ranges of *Antilocapra americana* and *Ovis canadensis* have been altered to an unknown extent since the advent of European civilization in Utah.

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Range maps for mammals in Utah generally were based on those published by Durrant (1952) and refined using distributional records from the following more recent papers: Anderson 1955, 1959, Armstrong 1972b, 1974, Behle and Hansen 1951, Benson 1954, Black 1970, Brown 1971, in press, Dearden and Lee 1955, Durrant and Hansen 1954, Durrant and Newey 1953, Durrant and Lee 1955, 1956, Durrant, Lee, and Hansen 1955, Durrant and Dean 1959, 1960, Easterla 1965, 1966, Egoscue 1961, 1966, Egoscue and Lewis 1968, Hansen 1953, Harris 1974, Hayward and Killpack 1956, 1958, Hennings and Hoffmann, in press, Genoways and Jones 1967, Keegan 1953, Killpack 1955, Krutsch and Heppenstall 1955, Lee 1960, Lee and Durrant 1960, Lowery and Egoscue 1968, Miller and Kellogg 1955, Musser and Durrant 1960, Nichols et al. 1975, Poché 1975, Poché and Bailie 1974, Poché and Ruffner 1975, Rasmussen and Chamberlain 1959, Shippee and Egoscue 1958, Stock 1970, Thaeler 1972, Wauer 1966, White 1953, Wood 1958. An attempt was made to make range maps at least roughly comparable in their level of resolution. As a check on the redrafted range maps, range limits in Utah were compared to those reported in adjacent states of Idaho (Davis 1939), Nevada (Hall 1946), Arizona (Cockrum 1960), Wyoming (Long 1965), Colorado (Armstrong 1972a), and New Mexico (Findley et al. 1975) and refined where appropriate.

Maps of continental ranges were based on those in Hall and Kelson (1959) with limits in Utah and adjacent states refined on the basis of more recent publications (Cockrum 1960, Long 1965, Armstrong 1972a, Findley et al. 1975) and maps of ranges in Utah prepared for the present paper.

Nine species have been documented in Utah since Durrant's (1952) checklist was published: *Sorex cinereus* (Durrant and Newey 1953), *Sorex nanus* (Durrant and Lee 1955), *Notiosorex crawfordi* (Wauer 1966), *Myotis thysanodes* (Krutsch and Heppenstall 1955), *Idionycteris phyllotis* (Black 1970), *Spermophilus richardsonii* (Hansen 1953), *Perognathus penicillatus* (Stock 1970), *Perognathus fasciatus* (Hayward and Killpack 1956), and *Odocoileus virginianus* (Miller and Kellogg 1955). Two other kinds, *Eutamias umbrinus* (White 1953) and *Thomomys idahoensis* (Thaeler 1972) have been accorded specific status. This brings to 126 the total number of species of recent mammals known from Utah. Most of these species were included by Sparks (1974) in a recent popularized checklist of the mammals of the state. Nomenclature in this paper follows Jones et al. (1975) and Hennings and Hoffmann (in press).

Work on mammals of Canyonlands National Park, of which the present study is a by-product, has been supported by the Society of the Sigma Xi, the Penrose Fund of the American Philosophical Society, the Council on Research and Creative Work of the University of Colorado, and the Canyonlands Natural History Association. I thank Dr. G. L. Kirkland, Jr., for helpful comments on an earlier draft of this paper. The paper is dedicated to the memory of

Stephen D. Durrant, late dean of mammalogists of the Intermountain West.

Results and Discussion

Distributional limits of mammalian species form complex but recurring patterns. These patterns may be described at various levels of resolution and by various means. In a local area, for example, one might be interested in the pattern of habitat requirements of a single species' population, in recurring communities of organisms, or in distribution along altitudinal or other gradients. On a broader scale, concern might be with distribution of species through ecological community types, with ecogeographic units (like the biotic provinces of Dice, 1943) that summarize regional ecological pattern, or with the shapes of species' ranges (areographic analysis). Emphasis here is on ecogeographic and areographic analysis, and the relationships between them. Ecogeographic description summarizes broad environmental patterns; areographic analysis may provide historical clues to the evolution of regional faunas (Armstrong 1972a).

Ecogeographic Considerations.— J. A. Allen (1892) pioneered ecogeographic studies of North American mammals, and Kendeigh (1954) reviewed subsequent work. Dice (1943) developed the concept of the Biotic Province to describe coherent units of regional landscape. Hagmeier and Stults (1964) and Hagmeier (1966) derived "mammal provinces" in North America by numerical methods, based on range maps in Hall and Kelson (1959). Hagmeier (1966) included parts of Utah in six mammal provinces, arranged in his hierarchy of ecogeographic units as follows:

- I. Coniferan Subregion
  - A. Mountain Superprovince
    - 1. Coloradan Province
- II. Sonoran Subregion
  - A. Navajo Superprovince
    - 1. Navajonian Province
    - 2. Uintian Province
  - B. Mapimi Superprovince
    - 1. Kaibabian Province
  - C. Columbia Superprovince
    - 1. Columbian Province
    - 2. Artemisian Province

The fact that the six provinces in Utah were arranged in four different superprovinces underscores the patent faunal heterogeneity in Utah detailed below.

Durrant (1952) outlined "faunal subdivisions" of Utah as follows (also see Fig. 1):

- I. Middle Rocky Mountain Faunal Area
  - A. Wasatch Mountain Province
  - B. Uinta Mountain Province
  - C. High Plateau Province
    - 1. Northern High Plateau Subcenter
    - 2. Southern High Plateau Subcenter
- II. Southern Rocky Mountain Faunal Area
  - A. Coloradan Province
    - 1. La Sal Mountain Subcenter
    - 2. Abajo Mountain Subcenter
- III. Colorado Plateau Faunal Area
  - A. Canyonlands Province
    - 1. Kaiparowits Subcenter
    - 2. San Rafael Subcenter
    - 3. Grand Valley Subcenter
    - 4. San Juan Subcenter
    - 5. Painted Desert Subcenter
      - a. Monument Valley District
      - b. Navajo Mountain District
  - B. Virgin River Valley Province
    - 1. Beaverdam Wash Subcenter
    - 2. St. George Subcenter

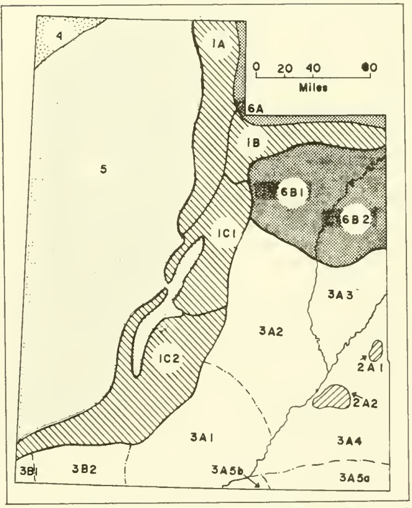

Fig. 1. Mammalian faunal subdivisions of Utah (after Durrant, 1952). For key to names of units, see text, p. 461.

IV. Columbia Plateau Faunal Area
V. Great Basin Faunal Area
VI. Northern Great Plains Faunal Area
  A. Bridger Basin Province
  B. Uinta Basin Province
    1. Duchesne Subcenter
    2. Uintah Subcenter

Durrant (1952) recognized these areas as distinctive because (1) certain species were restricted there and (2) because they acted as centers of differentiation for subspecies (p. 480). Boundaries of faunal areas were based on physiography. Although based mostly on distribution of mammals, Durrant's faunal areas are analogues of L. R. Dice's "biotic province," an ecogeographic unit that "... covers a considerable and continuous geographic area and is characterized by the occurrence of one or more ecologic associations that differ, at least in proportional area covered, from the associations in adjacent provinces" (Dice 1943: 3). Dice's units are based on distributional patterns in the biota as a whole, Durrant's on patterns in distribution and differentiation of mammals. Boundaries between both faunal areas and biotic provinces are zones of relatively rapid biotic change, zones in which limits of species tend to be concentrated (Armstrong 1972a). This fact was used in order to evaluate boundaries between faunal areas proposed by Durrant (1952: 480). A number of quantitative methods have been used in recent years to determine boundaries of faunal units, but faunal change in Utah is so rapid that useful units can be identified by inspection. Limits of ranges of 92 mammalian species were superimposed (Fig. 2). The concurrence between zones of rapid faunal change and ecogeographic boundaries is apparent from comparison of Figures 1 and 2. Each of the boundaries indicated in Durrant's map is marked by a concentration of limits in Figure 2. In particular, note the dense cluster of limits which outlines the central highlands and separates the Colorado Plateau on the east from the Great Basin in the west. In the northwestern corner of the state the Raft River Mountains are outlined clearly, as are the La Sal and Abajo Mountains in the southeast. A concentration of limits in the northeast suggests the distinctiveness of mammals of the Bridger Basin. In the west-central part of the state, the Deep Creek Mountains are highlighted by a concentration of limits. Were sufficient data available on mammals of this and other isolated mountain ranges of the Great Basin—comparable to those provided by Lee (1960) for the highlands of southeastern Utah—subdivisions of the Great Basin Faunal Area might be recognizable. It should be reemphasized that this evaluation of the boundaries of Durrant's faunal units is based on species' limits, whereas Durrant used two criteria, species' occurrence and differentiation of subspecies; this difference in technique has little bearing on the faunal units recognized.

Relationships among various faunal divisions of Utah were analyzed by a method used previously for Coloradan mammals (Armstrong 1972a). Occurrence of 109 mammalian species (92 species for which limits in Utah can be drawn with reasonable confidence and 17 species that range virtually statewide) was tabulated in each of

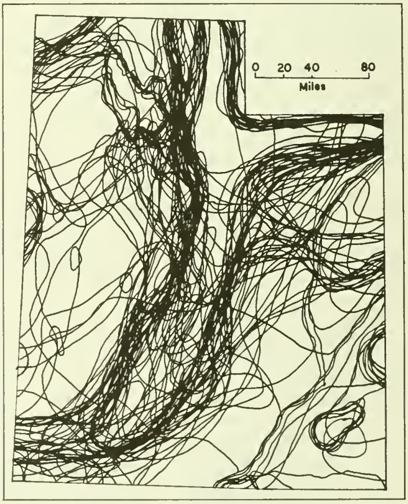

Fig. 2. Superimposed distributional limits in Utah of 92 mammalian species.

the 19 faunal units recognized by Durrant. Faunal resemblance was calculated by the formula $2C / N_1 + N_2$, where C is the number of species held in common between two units and N_1 and N_2 are total numbers of species in the two units. Resemblance values (which ranged from 0.438 to 0.964) were clustered by the unweighted pair-group method (Sokal and Sneath 1963: 309). Figure 3 is the result.

In large measure, the dendrogram substantiates the hierarchy of units suggested by Durrant (1952: 481—see p. 00 above), despite wide differences in technique and recent additions to knowledge of Utah mammals. Units of the Colorado Plateau form a tight cluster, with faunas of the Canyonlands and the Virgin River Valley separating into distinct subclusters, and units within the Canyonlands forming further subclusters east and west of the Colorado River. In the central mountainous core, two subclusters are evident. The Wasatch and Uinta mountains are more closely related than all but one other pair of faunal units, and the Northern High Plateaus and Southern High Plateaus form a distinct, albeit weaker, subcluster. The isolated La Sal and Abajo mountains form a distinct unit, allied (on average) more closely with the Colorado Plateau than with the central highlands of Utah. Their nearest contact with a well-developed highland fauna is via the high plateaus of western Colorado, not the Middle Rocky Mountains in Utah. The Duchesne and Uintah units of the Uinta Basin form a tight cluster and are distinct from faunal units of the Colorado Plateau south of the Tavaputs Plateaus, but they are more closely related to the Bridger Basin. The Great Basin and the Columbia Plateau (Raft River Mountains) tend to be faunally distinct from each other and from the rest of the state.

Comparison of Durrant's faunal units with the diagram in Figure 3 suggests that levels of the hierarchy (faunal area, province, subcenter, district) are not used quite consistently, at least at the specific level of analysis employed here. In particular, faunas of the Wasatch and Uinta Mountains are more closely related than most other pairs of units, yet they are distinguished as provinces. Recent studies (e.g., Durrant and Dean 1959) suggest that the Navajo Mountain and Monument Valley units are more distinctive than Durrant (1952) supposed. Indeed, Monument Valley seems to be more closely related to the San Juan area (which lies north of the San Juan River) than to the Navajo Mountain unit. Based on relationships in the dendrogram (Fig. 3), I suggest the following rough guidelines for levels of the hierarchy of ecogeographic units: average resemblance between faunal areas, less than 0.800; average resemblance between provinces within faunal areas, 0.800 to about 0.900; average resemblance between subcenters within provinces, greater than about 0.900. Using these criteria, the following slightly revised list of faunal subdivisions in Utah is suggested:

I. Central Highlands Faunal Area
    A. Middle Rocky Mountains Province
        1. Wasatch Mountains Subcenter
        2. Uinta Mountains Subcenter
    B. High Plateaus Province
        1. Northern High Plateaus Subcenter
        2. Southern High Plateaus Subcenter

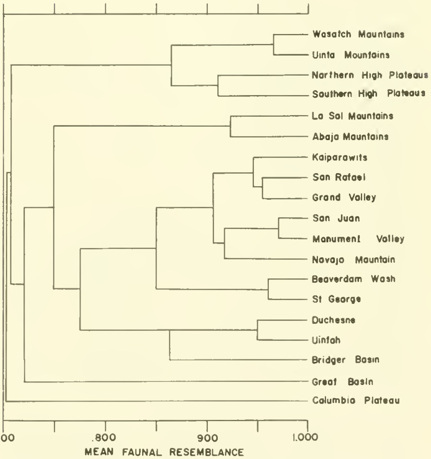

Fig. 3. Mean resemblance among mammalian faunal subdivisions of Utah. (For explanation of index, see text.)

II. Southern Rocky Mountains Faunal Area
A. La Sal Mountains Subcenter
B. Abajo Mountains Subcenter
III. Colorado Plateau Faunal Area
A. Canyonlands Province
1. Kaiparowits Subcenter
2. San Rafael Subcenter
3. Grand Valley Subcenter
4. San Juan Subcenter
5. Monument Valley Subcenter
6. Navajo Mountain Subcenter
Virgin River Valley Province
1. Beaverdam Wash Subcenter
2. St. George Subcenter
IV. Columbia Plateau Faunal Area
V. Great Basin Faunal Area
VI. Wyoming Basin Faunal Area
A. Bridger Basin Province
B. Uinta Basin Province
1. Uinta Subcenter
2. Duchesne Subcenter

Changes in names of two faunal areas (Middle Rocky Mountains to Central Highlands, Northern Great Plains to Wyoming Basin) follow Durrant's lead in naming faunal units to correspond with physiographic units (here following Fenneman, 1931).

Areographic Patterns.— Having considered distributional patterns of mammals in Utah and arrived at a set of ecogeographic faunal areas, let us turn to broader, continental patterns of distribution. The pattern of species' ranges, irrespective of extant ecologic pattern, may suggest historic affinities of the fauna. Udvardy (1969: 282) noted that the constituent species of a faunal list "... fall into groups with respect to the shapes of their geographic areas." These groups of species may be called "faunal elements." Polunin (1960: 212) suggested sorting out elements in a local flora as follows: (1) remove exotic and occasional species; (2) remove widespread species; (3) remove endemic species; and (4) sort out the remainder according to the shapes of their ranges. Such a procedure was used here, resulting in nine distinctive, areographic faunal elements and a group of widespread species.

The implications of these areographic faunal elements are complex. The area occupied summarizes the interaction of species' limits of tolerance with the mosaic of regional landscapes; both are subject to change over time. Hultén (1937) argued strongly that areographic analysis leads to historical insights in plant geography, promulgating the concept of "progressive equiformal areas," the common centers of which point to areas of origin (or refugia from environmental purturbations). Broad areographic studies of animals (e.g., Dunn 1931, for North American amphibians and reptiles, Mayr 1946, for birds, and Simpson 1947, and Burt 1958, for mammals) have used ranges—usually of higher taxonomic categories—as a basis for historical conclusions. A few studies have sought to use areographic patterns of species as clues to local faunal history. For example, Miller (1951: 582) recognized four avifaunal elements in California, "... on the basis of strong or repeated associations of species which have similar centers of distribution and probably also similar areas of origin." Armstrong (1972a: 333) discussed areographic patterns of Coloradan mammals, drawing tentative historical conclusions. Clearly, faunal elements may have a degree of historic integrity, reflecting centers of origin and dispersal, although recent ecologic history may have distorted older patterns. Despite problems in interpretation, the attempt to sort out areographic faunal elements is important. In the absence of a fossil record, such an exercise may provide the only clues to the development of the extant fauna.

Seventeen species (14 percent of the Utahan mammalian fauna) have ranges centering on the Middle Rocky Mountains (see Fig. 4A) and are called Cordilleran species. These are:

Sorex vagrans—Vagrant Shrew
Sorex monticolus—Dusky Shrew
Sorex nanus—Dwarf Shrew
Ochotona princeps—Pika
Eutamias amoenus—Yellow-pine Chipmunk
Eutamias umbrinus—Uinta Chipmunk
Marmota flaviventris—Yellow-bellied Marmot
Spermophilus armatus—Uinta Ground Squirrel
Spermophilus lateralis—Golden-mantled Ground Squirrel
Thomomys talpoides—Northern Pocket Gopher
Neotoma cinerea—Bushy-tailed Woodrat

Microtus montanus—Montane Vole
Microtus longicaudus—Long-tailed Vole
Arvicola richardsoni—Water Vole
Zapus princeps—Western Jumping Mouse
Ovis canadensis—Bighorn Sheep
Bison bison—Bison

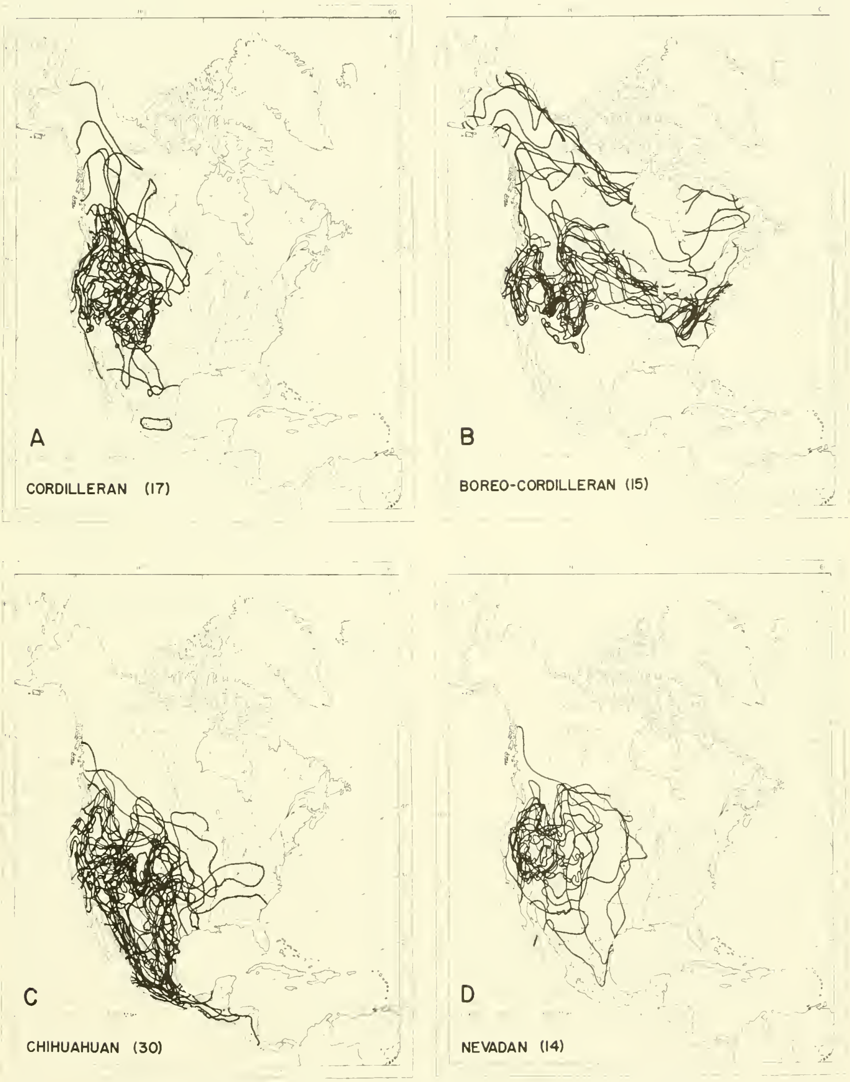
A
CORDILLERAN (17)
B
BOREO-CORDILLERAN (15)
C
CHIHUAHUAN (30)
D
NEVADAN (14)

Fig. 4 A-D. Superimposed continental distributions of species of four areographic faunal elements.

Ranges of most of these species extend from the Canadian Rockies southward, often in an increasingly insular pattern, to Arizona and New Mexico. They are restricted at their southern limits to mountainous country. Habitat of many of the species is mountain meadows, streamsides, and forest-edge situations. Two of the species (*Sorex obscurus* and *Spermophilus lateralis*) have isolated montane populations in Mexico. However, four other species (*Sorex vagrans*, *Eutamias amoenus*, *Spermophilus armatus*, and *Arvicola richardsoni*) do not extend farther south than the Middle Rocky Mountains, and they do not reach Colorado. The American bison of Utah were members of the subspecies *Bison bison athabascae* (see Hall and Kelson 1959: 1025) and hence are included as Cordilleran rather than widespread species.

The following 15 species of Utahan mammals (12 percent of the fauna) share a distributional pattern that may be called Boreo-Cordilleran:

Sorex cinereus—Masked Shrew
Sorex palustris—Water Shrew
Lepus americanus—Snowshoe Hare
Eutamias minimus—Least Chipmunk
Tamiasciurus hudsonicus—Red Squirrel, or Chickaree
Glaucomys sabrinus—Northern Flying Squirrel
Clethrionomys gapperi—Southern Red-backed Vole
Phenacomys intermedius—Heather Vole
Microtus pennsylvanicus—Meadow Vole
Martes americana—Marten
Martes pennanti—Fisher
Mustela erminea—Ermine
Gulo gulo—Wolverine
Felis lynx—Lynx
Alces alces—Moose

These species are distributed in mountainous parts of western North America and also eastward across the continent, mostly in forested areas (Fig. 4B). In an areographic sense, these species contrast markedly with those of the Cordilleran Faunal Element. Unlike Cordilleran species, many Boreo-Cordilleran mammals range throughout forested parts of Alaska and several species (including *Sorex cinereus*, *Mustela erminea*, *Gulo gulo*, *Felis lynx*, *Alces alces*) occur on both sides of Bering Strait. In addition, there is a tendency for Boreo-Cordilleran mammals to be associated with heavy forest. There is some suggestion that *Eutamias minimus*, perhaps the most euryecious mammal in this faunal element, may include more than a single species (Sutton and Nadler, 1969).

Thirty species (24 percent of the fauna) comprise the Chihuahuan Faunal Element:

Notiosorex crawfordi—Desert Shrew
Myotis californicus—California Myotis
Myotis yumanensis—Yuma Myotis
Myotis velifer—Cave Myotis
Myotis evotis—Long-eared Myotis
Myotis thysanodes—Fringed Myotis
Pipistrellus hesperus—Western Pipistrelle
Plecotus townsendii—Townsend's Big-eared Bat
Idionycteris phyllotis—Allen's Big-eared Bat
Antrozous pallidus—Pallid Bat
Tadarida brasiliensis—Brazilian Free-tailed Bat
Tadarida macrotis—Big Free-tailed Bat
Sylvilagus audubonii—Desert Cottontail
Lepus californicus—Black-tailed Jackrabbit
Eutamias dorsalis—Cliff Chipmunk
Spermophilus spilosoma—Spotted Ground Squirrel
Spermophilus variegatus—Rock Squirrel
Perognathus flavus—Silky Pocket Mouse
Dipodomys ordii—Ord's Kangaroo Rat
Reithrodontomys megalotis—Western Harvest Mouse
Peromyscus boylii—Brush Mouse
Peromyscus truei—Pinyon Mouse
Peromyscus difficilis—Rock Mouse
Neotoma albigula—White-throated Woodrat
Neotoma mexicana—Mexican Woodrat
Microtus mexicanus—Mexican Vole
Vulpes macrotis—Kit Fox
Urocyon cinereoargenteus—Gray Fox
Bassariscus astutus—Ringtail
Spilogale gracilis—Western Spotted Skunk

These species mostly occur in arid to semiarid grasslands or in rocky, broken brushlands or woodlands. They share a center of coincidence in the basin and range region of Chihuahua and Coahuila, Mexico, and Trans-Pecos Texas (Fig. 4C). Of this faunal element, four species (*Plecotus townsendii, Tadarida brasiliensis, Reithrodontomys megalotis*, and *Urocyon cinereoargenteus*) range east of the Mississippi River. However, their identification in the southwest with this faunal element is clear. The two species of free-tailed bats, *Tadarida brasiliensis* and *T. macrotis*, occur widely in South America, as does *Urocyon cine-*

reoargenteus. These might have been segregated as a Neotropical Faunal Element, inasmuch as only four of the remaining Chihuahuan species *(Myotis velifer, Peromyscus boylii, Neotoma mexicana, Spilogale gracilis)* range farther south than the Isthmus of Tehuantepec. Note that 12 of the Chihuahuan species (40 percent) are bats. Despite their capacity for flight these species are of restricted distribution, present patterns perhaps reflecting the historical integrity of this faunal element.

A Nevadan Faunal Element (Fig. 4D), comprised of the following 14 species, with a center of coincidence in Nevada, contributes 11 percent of the Utahan fauna:

Sorex merriami—Merriam's Shrew
Myotis volans—Long-legged Myotis
Euderma maculatum—Spotted Bat
Sylvilagus idahoensis—Pygmy Rabbit
Sylvilagus nuttallii—Nuttall's Cottontail
Lepus townsendii—White-tailed Jackrabbit
Spermophilus townsendii—Townsend's Ground Squirrel
Spermophilus beldingi—Belding's Ground Squirrel
Perognathus parvus—Great Basin Pocket Mouse
Microdipodops megacephalus—Dark Kangaroo Mouse
Dipodomys microps—Chisel-toothed Kangaroo Rat
Onychomys leucogaster—Northern Grasshopper Mouse
Lagurus curtatus—Sagebrush Vole
Antilocapra americana—Pronghorn

This is a complex distributional element. At a finer level of analysis it might be subdivided profitably. Some species are restricted to arid interior basins of the western United States (e.g., *Spermophilus townsendii, Microdipodops megacephalus, Dipodomys microps*), whereas others inhabit sagebrush steppe (e.g., *Sorex merriami, Sylvilagus idahoensis, Sylvilagus nuttallii, Lagurus curtatus*). *Lepus townsendii, Onychomys leucogaster,* and *Antilocapra americana* have an additional center of co-occurrence on the central Great Plains and might be considered a part of a Campestrian Faunal Element (Armstrong 1972a: 356), although this designation would not be particularly meaningful with respect to these species as they occur in Utah, inasmuch as communication with the Great Plains is indirect.

Twelve species (10 percent of the fauna) have continental distributions that might be called "Yuman," for their center of coincidence is in the Mojave Desert and along the Lower Colorado River in California, Arizona, Sonora, and Baja California (Fig. 4F). These species are:

Ammospermophilus leucurus—White-tailed Antelope Squirrel
Thomomys bottae—Botta's Pocket Gopher
Perognathus longimembris—Little Pocket Mouse
Perognathus formosus—Long-tailed Pocket Mouse
Perognathus penicillatus—Desert Pocket Mouse
Perognathus intermedius—Rock Pocket Mouse
Dipodomys deserti—Desert Kangaroo Rat
Dipodomys merriami—Merriam's Kangaroo Rat
Peromyscus eremicus—Cactus Mouse
Peromyscus crinitus—Canyon Mouse
Onychomys torridus—Southern Grasshopper Mouse
Neotoma lepida—Desert Woodrat

In the vicinity of the center of coincidence, *Ammospermophilus leucurus* and *Perognathus formosus* only occur west of the Colorado River, and *Perognathus intermedius* is known only east of the river. Yuman mammals generally do not range southward in Mexico as far as Chihuahuan species, with only five reaching Jalisco, Guanajuato, and San Luis Potosí. On the north, most species reach no farther than southeastern Oregon and southwestern Idaho, and several reach limits in Nevada and Utah. Note that half the species in this faunal element are heteromyid rodents, whereas the predominant rodents in the Chihuahuan element are cricetids. This fact underscores the historical integrity of these faunal elements.

Five species, comprising 4 percent of the Utahan mammalian fauna, constitute an Arizonan Faunal Element (Fig. 4F). These are:

Eutamias quadrivittatus—Colorado Chipmunk
Cynomys gunnisoni—Gunnison's Prairie Dog
Sciurus aberti—Abert's Squirrel
Perognathus apache—Apache Pocket Mouse
Neotoma stephensi—Stephens' Woodrat

These are species of the Four Corners area (although *Neotoma stephensi* is as yet unknown from Colorado, Armstrong 1972a: 312). In Utah, Arizonan species generally are restricted to the southeastern part of the state; all but *E. quadrivittatus* occur only east of the Colorado and Green rivers.

Three mammals of the Great Plains (*Spermophilus tridecemlineatus*, *Perognathus fasciatus*, *Mustela nigripes*) have limited

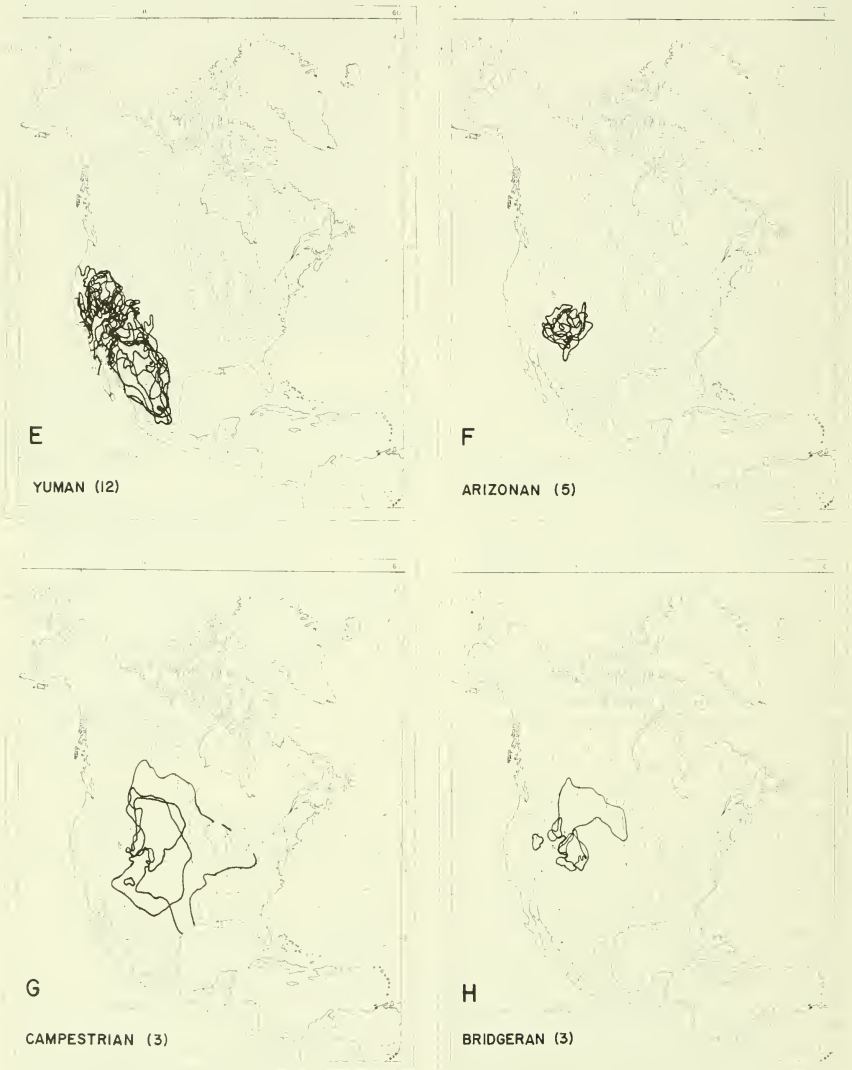
E
YUMAN (12)
F
ARIZONAN (5)
G
CAMPESTRIAN (3)
H
BRIDGERAN (3)

Fig. 4 E-H. Superimposed continental distributions of species of four areograhic faunal elements.

ranges in Utah and constitute a Campestrian Faunal Element (Fig. 4G). All occur in grasslands of the eastern part of the state. Another three species (*Cynomys leucurus, Thomomys idahoensis,* and *Spermophilus richardsonii*) share a center of coincidence in the Bridger Basin of southwestern Wyoming (Fig. 4H) and are herein called the Bridgeran Faunal Element. Armstrong (1972a: 354) placed *S. richardsonii* as a member of the Cordilleran Faunal Element, but its range is somewhat discordant with that group of species. Recent studies (Nadler et al. 1971) suggest that the population in Wyoming, Utah, and Colorado, known as *S. r. elegans,* is in fact specifically distinct from *S. richardsonii.* The range of *elegans* fits closely with the Bridgeran Faunal Element.

A single species of the mammalian fauna of Utah is obviously endemic there, *Cynomys parvidens,* the Utah Prairie Dog. According to Pizzimenti and Collier (1973), *C. parvidens* is more closely related to *C. leucurus* (a species of the Bridgeran Faunal Element) than to other prairie dogs; Collier and Spillett (1975) concluded that the range of the *C. parvidens* once covered large portions of the Great Basin.

Of mammals of Utah, the following 26 kinds (21 percent of the state's fauna) are sufficiently widespread (Fig. 4I) that they cannot be identified with any one areographic faunal element:

Myotis lucifugus—Little Brown Bat
Myotis leibii—Small-footed Bat
Lasionycteris noctivagans—Silver-haired Bat
Eptesicus fuscus—Big Brown Bat
Lasiurus cinereus—Hoary Bat
Lasiurus borealis—Red Bat
Castor canadensis—Beaver
Peromyscus maniculatus—Deer Mouse
Ondatra zibethicus—Muskrat
Erethizon dorsatum—Porcupine
Canis latrans—Coyote
Canis lupus—Gray Wolf
Vulpes vulpes—Red Fox
Ursus americanus—Black Bear
Ursus arctos—Grizzly Bear
Procyon lotor—Raccoon
Mustela frenata—Long-tailed Weasel
Mustela vison—Mink
Mephitis mephitis—Striped Skunk
Taxidea taxus—Badger
Lutra canadensis—River Otter
Felis concolor—Mountain Lion
Felis rufus—Bobcat
Cervus elaphus—Wapiti, or American Elk
Odocoileus hemionus—Mule Deer
Odocoileus virginianus—White-tailed Deer

Many of these species are rather large in size and many have broad habitat tolerances. It is perhaps noteworthy that half of these eurychores are members of a single order, Carnivora; carnivores are at least one step removed from direct dependence on the vegetation for food and generally are less narrowly restricted to particular habitats than are herbivores. Thirteen of the 23 carnivores known to occur in Utah are widespread species. In addition, three of four Utahn cervids are widespread on a continental scale. Three highly specialized aquatic species, the beaver, the muskrat, and the mink, appear on the list. This is hardly surprising, since aquatic habitats provide corridors of uniform habitat for dispersal through otherwise highly distinctive regions. Fewer than one-third of Utah's bats are widespread species; nearly 60 percent

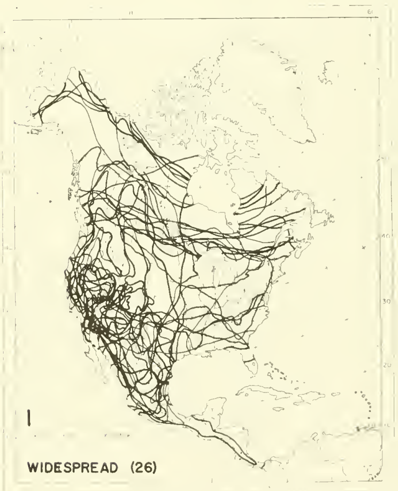

Fig. 4 I. Superimposed continental distributions of 26 widespread species.

are Chihauhuan kinds. Were distribution of bats better known, they might provide quite useful data for zoogeographers, contrary to the conventional wisdom.

The least broadly distributed species on the above list are the small-footed myotis (*Myotis leibii*) and the grizzly bear (*Ursus arctos*). The range of the former species is similar to that of those labelled "Nevadan," but it extends also across the Great Plains to the Ohio Valley and the East Coast. The former range of the grizzly bear extended eastward across the Northern Great Plains and Central Great Plains; otherwise the range is that of a Cordilleran species.

Figure 5 indicates cumulative percentage composition of the mammalian faunas of 19 ecogeographic faunal units by species of the 10 faunal elements identified by areographic analysis. Also indicated, for comparison, is the composition of the fauna of Utah as a whole, based on a total of 126 species. Only 109 species were tabulated in the faunal units, because of inadequate distributional data on 17 species (see Methods, above). Those species too poorly known to map represent five faunal elements: Cordilleran (three species), Boreo-cordilleran (one), Chihuahuan (four), Nevadan (three), and widespread (six). Thus, poorly known species are sufficiently well distributed across the major faunal elements that they do not bias the remarks that follow.

Note first in Figure 5 the consistent importance of widespread species at about 35 percent (28 to 38) through each of the faunal elements. It is the differential occurrence of species of well-defined areographic elements that makes the faunal units distinctive. Cordilleran species are most important in faunal units of the central mountain core of the state, somewhat less important in the La Sal Mountains and the Raft River Mountains of the Columbia Plateau. In other faunal units, their contribution falls to 10 percent or less. Boreo-cordilleran species are even more narrowly restricted to mountainous areas, although one species, *Eutamias minimus*, is sufficiently euryecious that it occurs in most faunal areas. "Boreal" mammals of Utah discussed by Brown (in press) mostly are Cordilleran and Boreo-cordilleran species as defined here.

The Chihuahuan Faunal Element is the largest distinctive areographic element in Utah, constituting about one quarter of the fauna. Given this prominence statewide, the element is under-represented in the central highlands faunal areas and on the Columbia Plateau. Over most of the Colorado Plateau south of the Tavaputs Plateaus, the Chihuahuan element contributes some 40 percent of the fauna. North of the Tavaputs Plateaus, in the southeastern mountains, and in the Great Basin, the importance of Chihuahuan species is diminished. Yuman mammals are most important on the southern Colorado Plateau, especially in the Virgin River Valley. They are absent from the Middle Rocky Mountain Province and from the Northern High Plateaus. Nevadan species, on the other hand, are most important in the Great Basin, with modest representation over most of the rest of the state (except on the Colorado Plateau, where they tend to be under-represented). The minor faunal elements tend to show rather narrow distribution across the state. Campestrian species occur in eastern Utah. Arizonan species occur mostly in the Canyonlands Province of the Colorado Plateau and in the Uinta Basin. Bridgeran species occur only in northeastern and east-central parts of the state.

Having considered the composition of the faunas of the ecogeographic units, it might be useful (if only as a check on the integrity of the faunal elements) to look briefly at the extent to which members of the 10 faunal elements occupy the various units (Table 1). Most of the units include 60 to 70 percent of the widespread species, with highest percentages occurring in mountainous areas. As might be expected, the units of the Central Highlands Faunal Area accommodate most members of the Cordilleran and Boreo-cordilleran elements, with occurrence attenuating southward. The Colorado Plateau includes the ranges of the highest proportion of Chihuahuan species. Yuman species, by contrast, occur strongly only in the Virgin River Valley, and Nevadan mammals are well represented only in the Great Basin. The minor faunal elements also are strongly represented only in local areas—Campestrian species in the northeast, Arizonan species east of the Colorado River (and south of its confluence with the Green River), the Bridgeran species in the Bridger Basin.

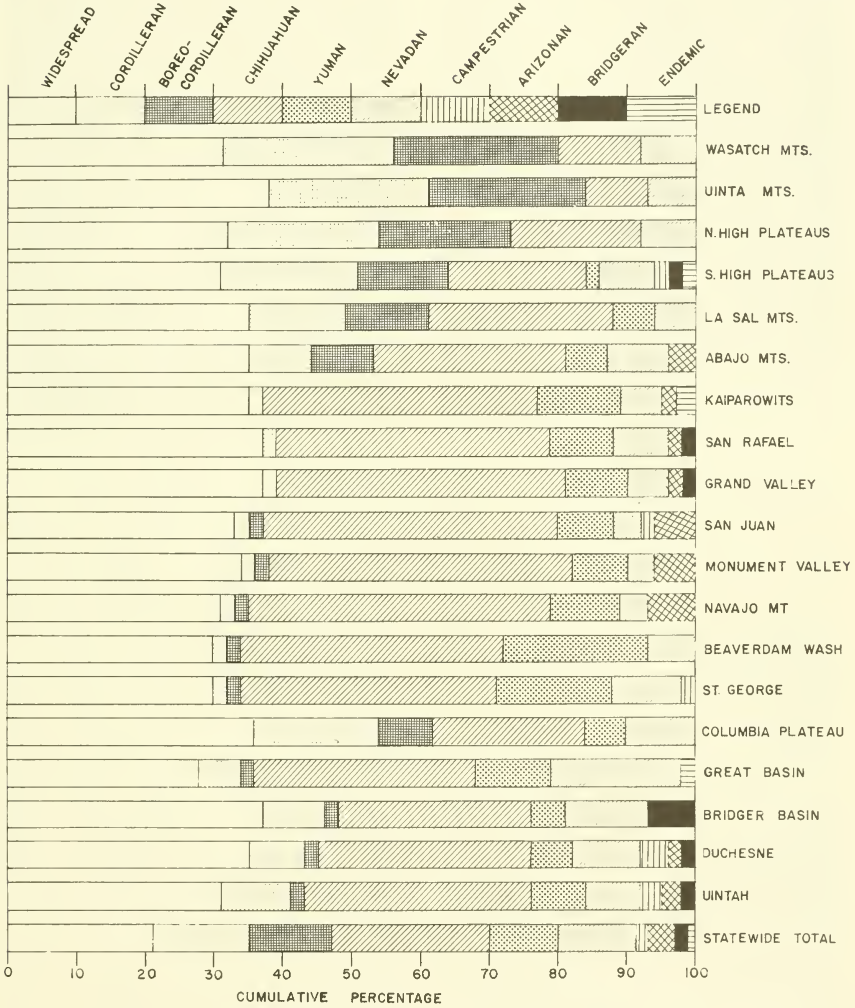

Fig. 5. Cumulative percentage composition of mammalian faunas of ecogeographic faunal areas by members of ten areographic faunal elements.

Historical Implications.— One of the major goals of zoogeographic analysis is to gain some insight into the evolution of local or regional faunas. Indeed, in the absence of an adequate fossil record, extant patterns of distribution and differentiation provide the only historical data that we have to work with. Durrant (1952) looked at patterns of subspecific differentiation in fossorial rodents as a clue to the Pleistocene history of the Bonneville Basin. Lee (1960) studied the distribution and differentiation of montane mammals of southeastern Utah and drew inferences about past faunal movements. Findley (1969) presented a strong argument on historical implications of such patterns in New Mexico and adjacent areas. Brown (1971, in press) analyzed distribution on several mountain ranges in Utah of mammals typical of woodland (and higher elevation) biotic communities, arguing convincingly that extant distributional patterns stem from local extinction of populations that reached the montane islands during the late Pleistocene. Armstrong (1972a) relied on evidence at both the specific and subspecific level to reach tentative historical conclusions about Coloradan mammals, and hypothesized access to the state by several faunal components under a diversity of environmental conditions which prevailed at various times in the past.

Extant zoogeographic patterns in western North America are a post-Pleistocene development. The Pleistocene Epoch was marked by pronounced climatic fluctuations. Warm, dry periods were interrupted by cool, moist glacio-pluvial intervals. Evidences of zoogeographic patterns in the earlier Pleistocene were obliterated by the last major glacial interval, the subsequent Hypsithermal Interval (Deevey and Flint 1957), and the development of the existing climatic regime (Armstrong 1972a). Extant patterns may provide clues to these most recent events. In the absence of a coherent or extensive fossil record, distributional patterns of recent species are the only clues available to

TABLE 1. Percentage of members of areographic faunal elements occurring in ecogeographic faunal units.

	Widespread	Cordilleran	Boreo-cordilleran	Chihuahuan	Yuman	Nevadan	Campestrian	Arizonan	Bridgeran	Endemic
Wasatch Mountains	69	82	93	23	–	29	–	–	–	–
Uinta Mountains	77	71	80	17	–	29	–	–	–	–
Northern High Plateaus	73	71	79	37	–	36	–	–	–	–
Southern High Plateaus	65	65	47	37	8	36	33	–	33	100
La Sal Mountains	69	47	40	43	25	21	–	–	–	–
Abajo Mountains	62	24	27	43	25	29	–	40	–	–
Kaiparowits	65	6	–	63	50	21	–	20	33	–
San Rafael	65	6	–	60	33	21	–	20	33	–
Grand Valley	65	6	–	63	33	14	–	20	33	–
San Juan	65	6	7	73	33	14	33	60	–	–
Monument Valley	65	6	7	73	33	14	–	60	–	–
Navajo	62	6	7	77	42	14	–	80	–	–
Beaverdam	62	6	7	67	92	29	–	–	–	–
St. George	58	6	7	60	75	29	33	–	–	–
Columbia Plateau	69	53	27	37	25	36	–	–	–	–
Great Basin	58	18	7	57	50	71	–	–	–	100
Bridger	62	24	7	25	17	36	–	–	100	–
Duchesne	65	24	7	50	25	36	67	20	33	–
Uintah	62	29	7	57	33	29	67	40	33	–

us. This is the case in Utah. Conspicuously lacking from the abundant literature on Pleistocene environments of Utah is any record of a mammalian local fauna. Even fragmentary fossils are few. When a nearly adequate fossil local fauna does become available (the Hogup Cave deposits from Box Elder County described by Durrant, 1970, and dated at 8500 years B.P.) the mammals that are present are those that would be expected in the vicinity of the cave today.

For purposes of discussion of Pleistocene conditions, Utah is conveniently divisible into three broad sections: the Great Basin, the central mountainous core, and the Colorado Plateau. The Great Basin records evidence of a series of pluvial periods separated by intervals of dessication (for details, see Morrison 1965). Lake levels fluctuated in synchrony with alpine glaciers in the higher mountains of central and northern Utah. This glaciation strongly influenced the modern landscape, lowering regional snowlines some 4000 ft, and producing summer temperatures perhaps 16 F cooler than today (Richmond 1965). On the Colorado Plateau, glacial intervals were marked by erosion, and warmer, drier periods produced sedimentary deposition (Kottlowski, Cooley, and Ruhe 1965). These events and conditions set an environmental baseline against which present distributional patterns of mammals have developed. During the last glacio-pluvial stage, conditions probably prevailed that were beyond the tolerance of many species in the fauna today. Previous patterns of distribution would have been obscured. With a depression of zonal biotic communities, forested situations that are highly disjunct today would have been more nearly continuous, and semidesert and desert community-types would have seen concommitant restriction and fragmentation.

The present-day fauna of the highlands of Utah provides better evidence of past environmental change than do faunas of the Colorado Plateau and the Great Basin. Today, a number of the state's mountain ranges and high plateaus appear as "islands" in a "sea" of nonmontane habitats. Communication among them by nonvolant mammals restricted to forested habitats is probably impossible. Nonetheless, some of the highlands have reasonably complete highland faunas (Brown 1971, in press). Altitudinal depression of zonal biotic communities by 2000 to 4000 ft would unite many of these areas with corridors of suitable habitat. The La Sal Mountains would have been connected with the Uncompahgre Plateau and the San Juan Mountains (and nearby ranges), and the Abajo Mountains probably would have been joined with the La Sals by more-or-less continuous forest or woodland corridors. Navajo Mountain, south of the San Juan River, and the Henry Mountains probably have been isolated (or nearly so) throughout Pleistocene times (although Lee, 1960, noted some affinity of mammals of the Henrys with those of the Aquarius Plateau). The distribution of forest-dwelling mammals along the mountains of central Utah suggests that Pleistocene conditions there provided a continuous corridor for movement. Isolated ranges of the Great Basin generally support depauperate highland faunas (Brown 1971, in press), although the definitive study of mammals of the minor ranges of southwestern Utah (House Range, Wah Wah Mountains, etc.) remains to be made.

The fact that faunas of the more isolated ranges on either side of the central highlands corridor have variously depauperate faunas probably reflects local extinction rather than selective or chance dispersal across barriers. The fact that such extinction has been more pronounced on the smaller uplifts may reflect the greater susceptibility of small populations to extinction (Brown 1971, in press). Such small populations would have been constricted still further by the climatic changes of the Hypsithermal Interval (warmer and effectively or absolutely drier than at present) which would have resulted in upward movement of zonal biotic communities with consequent restriction of the higher zones.

At lower elevations in Utah, extant distributional patterns strongly reflect present-day physiography, suggesting the efficacy of existing boundaries throughout the period of development of the fauna. Ranges of many Chihuahuan and Yuman species, for example, are limited on the Colorado Plateau by the major rivers and their canyons, despite the fact that seemingly suitable habitat often exists on the other side of the barrier. On a north-south axis, the Wasatch Mountains and the high plateaus today form an effective barrier to communication between the Great Basin and the Colorado Plateau. This barrier seems to have been generally effective throughout the period of evolution of the fauna. If the Hypsithermal Interval had significantly reduced its effectiveness, one would expect to find several Nevadan species on the Colorado Plateau. However, only the most euryecious species are found on both sides of the mountains. The Uinta Mountains also seem to have persisted as an effective barrier as faunal patterns have evolved. Bridgeran species are not found on the Colorado Plateau to any significant extent, and most Chihuahuan species are limited south of the Uintas.

A barrier to one faunal element or species may well be a corridor for the movement of another. The central mountainous corridor has been discussed in this context. The river systems of the Colorado Plateau seem generally to have been ineffective as corridors. Often they are entrenched deeply; riparian habitats tend to be fragmented or nonexistent. Species adapted to the broken habitats of the canyons seem to have found the river systems more effective corridors than have species of desert grasslands (such as several Yuman species).

Kelson (1951) suggested that the Colorado-Green system becomes an increasingly less effective zoogeographic barrier northward. East of the Colorado River and north of the San Juan, there is no strong barrier to northward faunal movement until one reaches the Book Cliffs. West of the Colorado, the Kaiparowits Plateau and the canyon of the Escalante River may constitute major barriers, but the mammals of this area remain poorly known except in the immediate vicinity of Lake Powell.

In summary, scrutiny of broad patterns of distribution of mammalian species provides few clues to the conditions of the past that influenced the composition of the extant fauna. Ranges of montane mammals suggest the occurrence of more continuous highland biotic communities in late Pleistocene time, and the depauperate faunas of isolated ranges may reflect the efficacy of the Hypsithermal Interval in constricting highland communities more severely than at present. In the lowlands, distributions correspond to extant barriers. Truly relict populations of lowland, xeric-adapted species are lacking. The overall conclusion must be that barriers to distribution in the present also were barriers to distribution in the past.

Summary

Distributional patterns of the 126 mammalian species native to Utah were analyzed and discussed. Ecogeographic faunal areas, proposed by Durrant (1952), were reevaluated. These correspond strongly with physiographic subdivisions of Utah. Areographic analysis indicated that several faunal elements contribute to the total mammalian assemblage within the political confines of Utah. These faunal elements contribute differentially to the several ecogeographic units, and they differ in their response to barriers and corridors for dispersal. With the exception of the montane fauna of the highlands of the state—which reflects both a cooler, moister late Pleistocene climate, and a warmer, effectively drier Hypsithermal climate—clues are lacking to suggest the vagaries of Quaternary history. Data still are inadequate to allow a satisfactory picture of some aspects of mammalian zoogeography in Utah. Areas of particular interest are the south-central part of the state (Kaiparowits Subcenter) and the isolated basins and ranges of the southern part of the Great Basin Faunal Area.

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A NEW FOSSIL SPONGE FROM THE ORDOVICIAN GARDEN CITY LIMESTONE OF SOUTHEASTERN IDAHO

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Abstract.— The new choristid demosponge, *Loganiella johnsoni*, is described from the upper part of the Lower Ordovician Garden City Formation of southeastern Idaho. The new sponge is a relatively thin walled, low, subcylindrical form. The skeletal net is composed of tracts of curved rodlike spicules, but details have been lost on all specimens because of extensive silicification. Impressions, however, suggest a close relationship to the choristid *Dystactospongia* Miller, 1889.

Several specimens of a new sponge were collected from the Ordovician Garden City Limestone by Victor Church during a study of the Preston Quadrangle in southeastern Idaho in 1941. He was assisted by Chester O. Johnson of Gustavus Adolphus College during the study. Dr. Johnson kindly loaned us the collection of sponges he made at that time. A collection of sponges was also given to Utah State University by Mr. Church. These sponges were loaned to us by Dr. J. Stewart Williams and incorporated in this study.

The Garden City Formation was named for exposures in the Bear Lake region of northern Utah and southeastern Idaho by G. B. Richardson (1913: 407–408, 1914: 13–16) and includes the Lower Ordovician beds between the underlying Cambrian St. Charles Limestone and the overlying Swan Peak Quartzite. The formation is approximately 900 feet thick in the type section, which is approximately 15 miles east of the locality where the sponges were collected.

The Garden City Limestone was later restudied in detail by R. J. Ross, Jr. (1949, 1951). He described the fauna and zoned the formation utilizing the moderately abundant trilobites and other fossils and established an alphabetic zonation, parallel to that utilized by Hintze (1951, 1952) for equivalent beds of the Pogonip Group in western Utah and eastern Nevada.

The fossils were collected from E ½, NW ¼, SE ¼ Section 30, Township 16 South, Range 42 East, in southern Franklin County, southern Idaho (Map 1). The locality is along the west face of Crab Ridge near the ridge crest, .2 mi. north of the Utah-Idaho boundary. Crab Ridge is a prominent linear feature along the east side of the headwaters of Logan River.

Johnson (1962, pers. comm.) notes that there are no major outcrops in the wooded slope along the east side of Logan River valley near where the sponges were collected from talus fragments. There seems little question, however, that the material came from near the crest of Crab Ridge because of the location of the talus on the slope.

The sponges are silicified and some of the better specimens were etched free of matrix by dissolving the limestone in dilute acetic acid. Many small, spherical, *Hindia*-like sponges(?) were recovered in the residue, along with numerous conodonts. The conodonts were sent to Dr. Raymond L. Ethington of the Department of Geology, University of Missouri for identification and zonation. Ethington and Clark (Hintze 1977) have established a conodont zonation for the Pogonip Group in western Utah and eastern Nevada and have tied this to the trilobite zones of Hintze and Ross (1950). On the basis of the conodonts the sponges came from rocks of zone J to L (Ethington, 1977, pers. comm.).

Conodonts recovered from the matrix around the holotype (BYU 1090) include the following forms, identified by Ethington:

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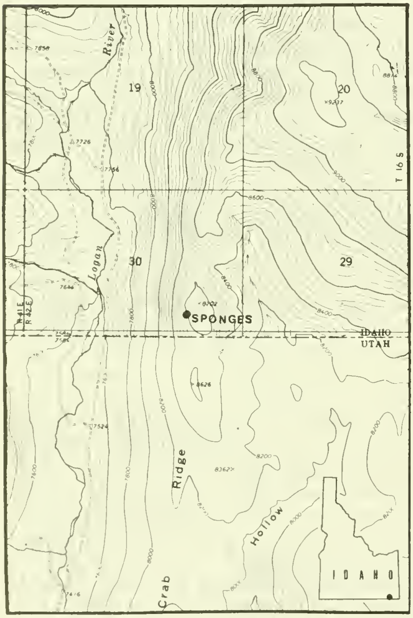
?*Drepanoistodus* sp.
Microzarkodina aff. *M. flabellus* (Lindstrom)
"Scandodus" robustus Serpagli
Scolopodus gracilis Ethington and Clark
?*Walliserodus* aff. *W. comptus* (Branson & Mehl)
New Genus A of Sweet, Ethington, & Barnes, 1971
New Genus B of Sweet, Ethington, & Barnes, 1971

Those conodonts recovered from matrix around the figured paratype (BYU 1091) include the following forms, identified by Ethington:

?*Acodus* sp.
?*Drepanoistodus* sp.
Microzarkodina aff. *M. flabellus* (Lindstrom)
Oistodus multicorrugatus Harris
Protopanderodus sp. s. f.
Scolopodus gracilis Ethington & Clark
New Genus A of Sweet, Ethington, & Barnes, 1971
New Genus B of Sweet, Ethington, & Barnes, 1971

Ethington (1977, pers. comm.) notes that "*Oistodus multicorrugatus* and *Scolopodus gracilis* have rather long ranges and are of little help for stratigraphic interpretation. Fortunately some of the forms are quite diagnostic. In particular, New Genus A, New Genus B, *Microzarkodina* aff. *M. flabellum*, and '*Scandodus*' *robustus* occur together in the Wah Wah and Juab Formations. New Genus A and '*Scandodus*' *robustus* are present in the basal Whiterockian (*Orthidiella* Zone) in the Monitor Range, central Nevada, which is the equivalent of Zone L in the Ibex area of western Utah. . . . Clearly these conodonts represent a stratigraphic level near the top of the Canadian Series or near the bottom of the Whiterockian Stage. Until this series boundary between the Lower and Middle Ordovician has been defined more precisely, one cannot be more specific. In terms of the Hintze-Ross zonal scheme for shelly fossils they represent the general range of Zones J, K, and L."



Map 1. Index map to the type locality of the new Ordovician sponge *Loganiella johnsoni* Rigby and Gilland. The sponge came from upper beds of the Garden City Formation, from talus blocks, on the east side of Logan River canyon.

SYSTEMATIC PALEONTOLOGY

Class DEMOSPONGIA Sollas, 1875
Order CHORISTIDA Sollas, 1888
Family uncertain
Loganiella, n. gen.

DIAGNOSIS.— Cylindrical to subcylindrical sponges with a flat base, a moderately thick wall, and a simple wide-open spongocoel. Relatively small canals feed radially, through the wall into the spongocoel. The skeletal net is composed of curved oxeas(?) that produce tracts with reticulate pattern that has a dominant radial structure.

DISCUSSION.— At first glance, these forms appear similar to flat-crested *Receptaculites*, but the skeletal structure and the canal pattern is so distinctly dissimilar that the forms are clearly unrelated.

Perhaps the most closely related genus is *Dystactospongia* (Miller 1882: 42). In Miller's original description the spicule structure was poorly defined, but in a subsequently discovered specimen of *Dystactospongia madisonenses* Foerste, described by Rigby (1966), the spicule pattern is preserved. In this latter specimen, the skeletal net appears as a confused mass of fibrous spicules at first glance, but is composed of closely spaced spicules which intertwine—almost like a batch of spaghetti. Individual spicules line the canal openings, much as in the present specimens. *Dystactospongia* is a massive lobate, or digitate, to semiglobular form, however, in contrast to the simple, open, thin-walled, bowl shape of the present sponge. If our interpretation of the spicule pattern on the Idaho specimens is correct and the forms are related to *Dystactospongia* from the Ordovician of the midcontinent, *Loganiella* should be included in the Order Choristida in the Class Demospongia.

Etymology.— The genus *Loganiella* is named after the Logan River, where the type material was recovered.

Type species.— *Loganiella johnsoni.*

Loganiella johnsoni, n. sp.

Figs. 2-6

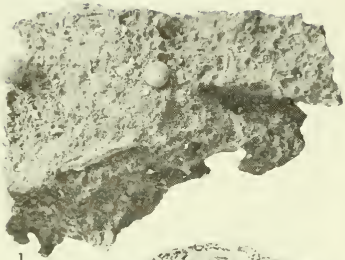
Description.— Bowl-shaped to cup-shaped subcylindrical sponges (Fig. 1) with a flattened base and nearly vertical to slightly inclined walls that surround a simple, broad, open spongocoel. The base of the sponge is slightly concave to nearly flat, but with a rounded margin. From the rounded margin of the base, the walls extend vertically to slightly inclined inward for approximately 3 cm to the upper edge of the fragment.

The holotype (BYU 1090; Figs. 3, 5, 6) is nearly circular, when viewed from above, and has a maximum diameter of 72 mm. The base is slightly warped, possibly during growth because the spicule net apparently is solidly fused and the sponges appear to show little distortion. Wall thickness is moderately uniform, ranging from 3.7 mm at the thin oscular(?) margin up to a maximum of 4.5 mm where the flat base curves upward into the subcylindrical wall.

A paratype (BYU 1091; Figs. 2, 4) is of the same general shape and has a maximum diameter of 70 mm and is from 20 to 22 mm high. The base of the sponge is approximately 10 mm thick. The wall thickens to a maximum of 15 mm at the lower-most margin of the spongocoel but then thins to only 5 to 6 mm at the upper edge of the preserved fragment. In the paratype a moderately long section of what is considered to be the upper oscular rim is preserved. It has a rounded, although somewhat channeled, upper surface. The wall structure shows well completely around the upper edge. Where the wall has been broken and irregularly silicified the radial canal pattern shows moderately well.

The canal pattern shows best in the holotype where four different sizes of openings are present. The largest of these occur on the exterior of the base and they are particularly well defined in an area newly etched free of matrix. These large canals are circular to elliptical. They are particularly elliptical where two canals appear to converge to form one circular opening within the interior. Circular single canals range from 0.20 mm to 0.6 mm in diameter. These canals are separated by relatively thick skeletal tracts that range from 0.3 to 1.5 mm across. This particular canal series is spaced moderately irregularly over the surface, but in some areas occurs in an almost rectangular pattern. In a characteristic area 5 mm square there are from 20 to 25 of the larger canal openings. Where the pattern is moderately regular or linear they are spaced approximately 1 mm apart. There may be five or six of the larger canal openings per 5 mm, as measured along any one single series.

A second, smaller series of canals ranges from 0.15 to 0.30 mm in diameter. These occur irregularly within the skeletal tracts and appear to parallel or possibly converge with the larger canal openings in the interior of the wall. Where best preserved, these small canals are spaced from 0.4 to 0.6 mm apart along an individual skeletal tract but, in general, they occur in the dense skeletal net. Some of these openings are irregular and may be produced, in part, by irregularities of silicification. Others, however, are sufficiently circular and so well defined that they must indicate original openings in the net of the sponge. These canals are spaced from 0.1 to 0.2 mm apart in cross sections



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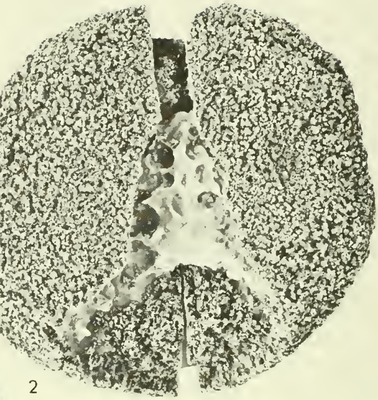

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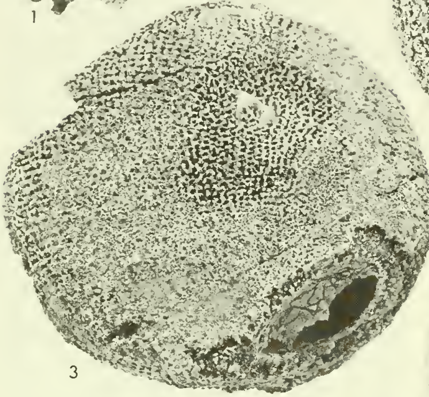

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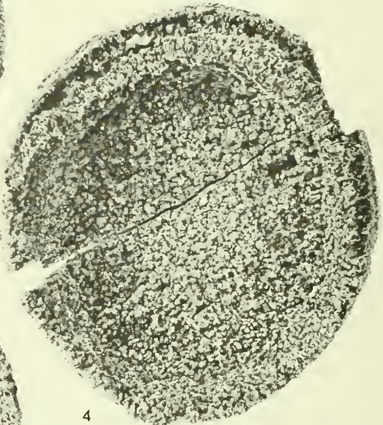

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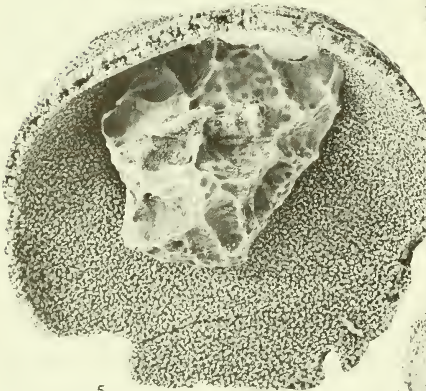

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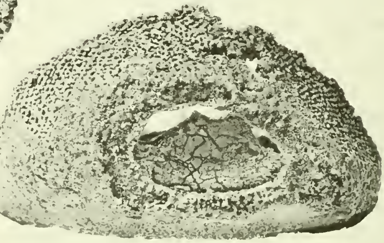

6

through the wall and, like the large canal series, appear to pass directly through the wall and to be almost straight.

The inner surface of the spongocoel is somewhat more irregular than the exterior and the canals there are poorly defined. Circular canals ranging from 0.25 to 0.6 mm in diameter occur on the silicified or encrusted interior wall. Most canal openings here range from 0.25 to 0.30 mm across, are terminations to the straight radiating canal series, and connect to the larger ostia on the exterior. These spongocoel openings, in general, are separated by skeletal tracts from 0.4 to 0.6 mm across. These tracts, like those on the exterior, have rounded cross sections so that the diameter of the canal openings flare at the immediate spongocoel surface but narrow a few tenths of a millimeter into the wall from the spongocoel margin.

Smaller openings, from 0.15 to 0.3 mm across, are also common and may represent inner termination of some of the large radiating canals.

The spongocoel margin has a somewhat frosted or rounded appearance, in contrast to the much more sharply defined canals and skeletal tracts of the exterior. The gastral or interior surface of the wall is irregularly porous and there is practically no pattern of canal placement, such as the linear pattern seen on the exterior.

Because of silicification, spicules in the interior of the tracts are not preserved, but impressions of the spicules are evident on the exterior of a few tracts, particularly on the spongocoel margin. They are curved to moderately straight rodlike spicules which appear to be diactines. It is impossible to tell in this preservation whether these are rhizoclone spicules with a smooth exterior facing toward the canals or whether they are oxeas or simple curved spicules as in *Dystactospongia*. These spicules are from 0.02 to 0.035 mm in diameter and up to 0.25 mm long, although on none can the total length be recognized because the tips are either broken or lost in the ropy fabric. Spicules are curved to outline the circular canals and lie tangential to the main fibers. On some tracts, where the spicules show particularly well, there are from 10 to 15 spicules coating the exterior. This would suggest that individual tracts may have as many as 50 to 75 spicules in a single cross section. The spicules generally are elongate, parallel to the long dimensions of the somewhat reticulate mesh. In the cross-connecting bars, for example, they are tangential to the spongocoel wall and cross-connect the tracts which are extending directly through the sponge wall. The spicule pattern is less clearly preserved on the exterior—a few spicules' impressions here and there—and the generally ropy appearance of the tracts is poorly expressed.

ETYMOLOGY.— The species is named in honor of Dr. Chester O. Johnson, who recognized the sponge origin of the material and made most of the collection available.

TYPE MATERIALS AND OCCURRENCE.— The

Figs. 1-6. Fossil sponges from the Garden City Limestone of southeastern Idaho: 1. Small spherical *Hindia*(?) associated with the holotype of *Loganiella*, from the Garden City Limestone, Logan River locality; 87 percent of natural size.

Figs. 2-6. *Loganiella johnsoni*. 2, 4, Paratvpe, BYU 1091. 2, Flat, coarsely silicified base of the paratype with some calcareous matrix in the sponge wall. 4, View from above into the simple spongocoel of the coarsely silicified paratype showing the moderately thick walls of this particular specimen. 3, 5, 6, Holotype BYU 1090. 3, View of the flat base of the holotype showing the somewhat rectangularly spaced skeletal tracts of the sponge. The opening at the lower right is an artifact of preservation. Small light triangular area in the upper right center is a residum of matrix. Spicules show under the microscope near the base of this remnant. 5, View down into the flat bottom of the spongocoel of the holotype, here partially encrusted by matrix. The thin wall of this specimen shows above, in the wall fragment in the upper part of the specimen. The distinctly nonpatterned openings of the canals on the interior of the sponge contrast sharply with the distribution seen in the basal part of the exterior. The artificial opening through the sponge wall here is at the top of the specimen. 6, Side view showing the characteristic flat base, rounded margins, subcylindrical to broadly conical walls, and the moderate regularity of canal spacing on the upper flanks of the sponge; 87 percent of natural size.

sponges are known, at present, only from the upper part of the Garden City Formation, in rocks of zone J to L, in southern Idaho. Holotype, BYU 1090, and paratype, BYU 1091.

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HOST-INDUCED MORPHOLOGICAL VARIATIONS IN THE STRIGEOID TREMATODE *POSTHODIPLOSTOMUM MINIMUM* *(TREMATODA: DIPLOSTOMATIDAE).* IV. ORGANS OF REPRODUCTION (OVARY AND TESTES), VITELLINE GLAND, AND EGG[1]

James R. Palmieri[2]

Abstract.— A variety of amphibian, reptilian, avian, and mammalian hosts were used in experimental development of *Posthodiplostomum minimum.* Results of this study indicate that the organs of reproduction (testes and ovary) as well as the vitelline gland and egg underwent host-induced morphological variations. Due to the lack of host specificity of *P. minimum* as well as the overlap of reported egg and body sizes of species of *Posthodiplostomum,* it is apparent that several reported species are not valid.

Throughout the literature, members of the trematode family Diplostomatidae have been classified and divided based upon the size and shape of the anterior and posterior testes, extent of vitelline gland, position of the ovary relative to the testes and the size of the egg (Dubois 1937, 1952, 1964, 1968, 1970). In the above cases, Dubois considered the strong host specificity supposedly demonstrated by strigeoids to be the basis for his extensive taxonomic revisions. In recent years several investigators have shown that strigeoid trematodes are not as physiologically host specific as previously suggested. Ulmer (1961) emphasized the need for additional experimental data relative to host specificity in order to assess the validity of Dubois's use of it as a major criterion for establishing taxonomic relationships. Palmieri (1973, 1975, 1976) clearly demonstrated that *Posthodiplostomum minimum is able to develop to a gravid state in many host species within all vertebrate classes except fishes. It is doubtful, however, that host specificity in a strict sense is of value in differentiating species of Posthodiplostomum.* Analysis of data presented in this paper clearly indicates that testes number, size and shape, ovary position, vitelline gland distribution and egg size undergo great morphological variations when experimentally developed in amphibian, reptilian, avian, and mammalian hosts. Similar results dealing with morphological variation have been reported by Watertor (1967), Blankespoor (1971), Kinsella (1971), Campbell (1973), and Palmieri (1973, 1975).

Material and Methods

The material and method section of this paper has been reported by Palmieri (1976).

Results and Discussions

Ovary.— Five variables were analyzed in studying the ovary of adult *P. minimum,* namely: (length, width, cross sectional area, ratio of length to width, and the variation in the position of the ovary relative to anterior and posterior testes). A complete analysis of the above data can be found in Table 1. Variations in ovary position of *P. minimum* are found in Figures 1-6 and Table 2.

The ovary of *P. minimum* commonly varies in position from anterior to the anterior testis (Figs. 1–2) to lateral (Fig. 3) or posterior (Figs. 4–6) to it. In worms recovered from all four classes of experimentally fed definitive hosts, the ovary was situated most commonly to the left of the anterior testis

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[1] See Part II of this study, Great Basin Nat. 37:137, 1977.

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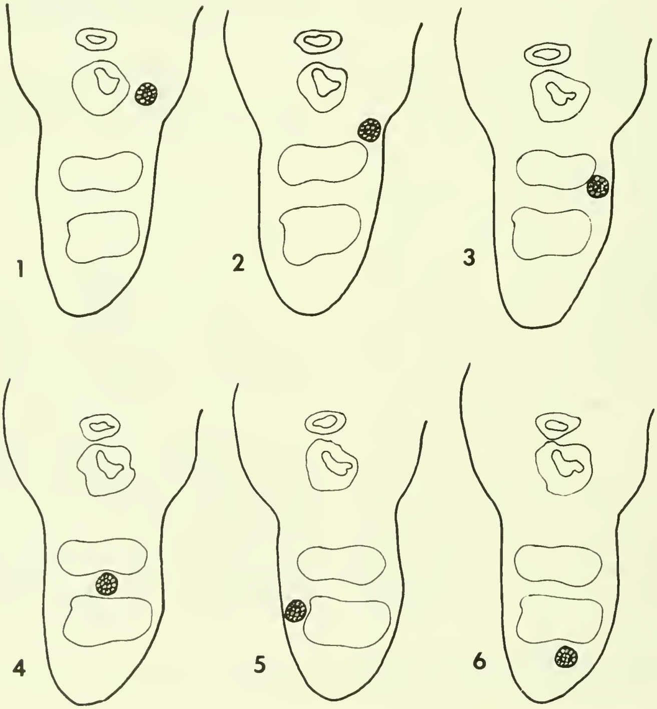
Table 1. Analysis of ovary measurements of *P. minimum* from experimental definitive hosts.*

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Ovary Length (OL)	0.027	0.007	0.029	0.013	0.031	0.030
Ovary Width (OW)	0.029	0.008	0.030	0.014	0.033	0.031
Cross-Sectional Area of Ovary (AOLXOW)	0.001	0.001	0.001	0.001	0.001	0.001
Ratio of Ovary Length to Width	0.882	0.241	0.930	0.542	0.940	0.976

*All measurements in mm.



Figs. 1-6. Variations in position of ovary as depicted in Table 2.

(Fig. 3). It was not uncommon to find the ovary in several of the above positions, however, within worms recovered from any given genus of cold-blooded definitive host. Variations such as these are much more common in poikilothermic than in homiothermic definitive hosts.

TESTES.— Ten variables were used in describing the size, number, and relationships of the anterior and posterior testes (anterior testes length and width, posterior testes

TABLE 2. Variation in ovary position relative to testes in adult *Posthodiplostomum minimum* recovered from experimental amphibian, reptilian, avian, and mammalian Hosts.

Experimental Host Class	Ovary Position Corresponding to Figures 1-6
Amphibia	2,3,5
Reptilia	2,3,6
Aves	1,2,3,4,5
Mammalia	2,3,4,5

TABLE 3. Analysis of testes measurements of *P. minimum* from experimental definitive hosts.°

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Anterior Testis Length (ATL)	0.048	0.017	0.042	0.031	0.066	0.057
Anterior Testis Width (ATW)	0.150	0.056	0.136	0.087	0.198	0.182
Posterior Testis Length (PTL)	0.050	0.017	0.048	0.027	0.068	0.053
Posterior Testis Width (PTW)	0.138	0.072	0.123	0.079	0.036	0.167
Cross-Sectional Area of Anterior Testis (AATLXPTL)	0.008	0.004	0.006	0.002	0.013	0.010
Cross-Sectional Area of Posterior Testis (APTLXPTW)	0.008	0.004	0.006	0.003	0.013	0.010
Ratio of Anterior Testis Length to Width (RATLPTW)	0.355	0.153	0.332	0.446	0.338	0.352
Ratio of Posterior Testis Length to Width (RPTLPTW)	0.408	0.399	0.527	0.251	0.371	0.308
Ratio of Cross-Sectional Area of Anterior Testis to Posterior Testis (RATXXPT)	1.016	0.658	1.174	0.522	1.067	0.989

°All measurements in mm.

length and width, cross-sectional area, ratio of testes length to width, ratio of the cross-sectional area of the testes, and testes number). An analysis of the above data can be found in Tables 3 and 4. A comparison of the morphological variation is drawn at the light level on Figures 9–21.[2]

The appearance of the testes, including their size, shape, and number, varied widely in specimens of *P. minimum* recovered from various vertebrate hosts. A definite trend is noticeable in accordance with the specific class of vertebrate host employed. In worms developed within avian hosts, anterior and posterior testes occupy a large area of the hindbody (Figs. 14, 16[2]) and are large, well developed, and approximately twice as wide as they are long. In mammalian hosts, worms have less normal-looking testes (Fig. 18[2]), but the latter are about three to four times as wide as long (Figs. 17, 21[2]), and are "dumbbell" shaped. Within poikilothermic hosts, testes of *P. minimum* appear even wider and sometimes show twists and diverticula (Figs. 11,13[2]). In several reptilian and mammalian hosts, no posterior testis appears. Several worms recovered from amphibian hosts showed no signs of testes development. Throughout all classes of hosts experimentally infected, worms from the more ecologically abnormal hosts tend to develop extremely wide testes with trends toward reduction in size of the posterior testis.

TABLE 4. Variations in testes number in adult *Posthodiplostomum minimum* recovered from experimental amphibian, reptilian, avian, and mammalian hosts.

Experimental Host Class	Testes Number
Amphibia	0,2
Reptilia	1,2
Aves	2
Mammalia	1,2

TABLE 5. Variation in vitelline gland distribution in adult *Posthodiplostomum minimum* recovered from experimental amphibian, reptilian, avian, and mammalian hosts.

Experimental Host Class	Vitelline Gland Distribution*
Amphibia	0,2,3
Reptilia	0,2,3
Aves	1,2
Mammalia	0,2,3

*0. No vitellaria present
1. From posterior region of the holdfast organ to region between acetabulum and oral sucker (corresponds to Fig. 13, Part III of this study).
2. From midregion of anterior testis to region between acetabulum and oral sucker (corresponds to Fig. 14, Part III of this study).
3. From midregion of holdfast organ to anterior region of acetabulum (corresponds to Fig. 15, Part III of this study).

VITELLINE GLAND DISTRIBUTION.— Only the distribution of vitelline glands in the forebody and hindbody was considered in the adult *P. minimum* recovered during this investigation. This data was reported and diagrammed in Figures 13-15, Part III of this study.

In most specimens of *P. minimum* recovered from avian hosts, vitelline follicles are large and granular. Follicles are most heavily concentrated in an area extending from a region equidistant between acetabulum and oral sucker to the anterior half of the anterior testis. In some amphibian, reptilian, and mammalian hosts, vitelline distribution is identical to that found in the avian hosts, but follicles are smaller and less granular. In worms recovered from some reptilian and avian hosts (*Chrysemys*, *Columba*, and *Gallus*), vitelline distribution is reduced to an area surrounding only the holdfast organ and the acetabulum. Worms recovered from amphibian hosts demonstrate a further reduction in vitelline distribution to a point where only a few follicles scattered around the holdfast are present. In some cases (amphibian, reptilian, and mammalian hosts) a complete absence of follicles resulted, even though age of the worms was sufficient to have permitted full development of these follicles.

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[2] See Part II of this study, Great Basin Nat. 37:137, 1977.

Egg.— Six variables were analyzed in evaluating measurements of the eggs of *P. minimum.* Linear measurements consisted of egg length and width from worm specimens within a single host class. Two relationships of the above data were also studied, namely the ratio of the egg length means to the egg width means and the mean value for the cross-sectional area. A complete analysis of the above data can be found in Table 6.

Egg shape and development of *P. minimum* vary among experimental poikilothermic and homiothermic definitive hosts utilized in this investigation. *P. minimum* eggs from amphibian and reptilian hosts are small and round. Those recovered from amphibian hosts were not viable and no miracidial development could be detected. Egg size was largest from worms recovered from homiothermic hosts. The largest and most viable eggs of *P. minimum* are recovered from piscivorous avian and carnivorous mammalian hosts, and such eggs are characteristically oval and operculate. Egg number per worm varies from 1–2 in amphibian and reptilian to 1–5 (typically 3) in avian and mammalian hosts.

One of the principal factors contributing to the complex problems of speciation within the genus *Posthodiplostomum* and perhaps other genera of digenetic trematodes has been the lack of experimental studies providing experimental data on host-induced variation at the intraspecific and interspecific levels. This study, based upon careful examination of over a thousand specimens of *Posthodiplostomum minimum* recovered from experimental hosts, emphasizes the pronounced morphological variation resulting from the rearing of *P. minimum* in different vertebrate definitive hosts, from any individual host class. Characters undergoing a significant change (F .01 level of significance or higher) include egg length and width, both ratio and area of the egg length means and the egg width means, and body length. These are the poorest characters for taxonomic identification of *P. minimum* since they show a significant morphological variation due to influences of the class of host in which development takes place.

This study provides evidence that the only significant morphological criteria for the determination of *Posthodiplostomum minimum* developed within any definitive host class are the ratio of the body length to body width, oral sucker cross-sectional area, acetabular index of length, acetabulum length, oral sucker width, and acetabulum width. Ratios between holdfast length and width and anterior testis length and width,

Table 6. Analysis of egg measurements of *P. minimum* from experimental definitive hosts.*

Variable	Mean of Combined Host Class	Standard Deviation	Means			
			Amphibian	Reptilian	Aves	Mammalia
Egg Length (EL)	0.078	0.007	0.034	0.025	0.084	0.085
Egg Width (EW)	0.030	0.054	0.028	0.020	0.058	0.057
Cross-Sectional Area of Egg (AELXEW)	0.004	0.005	0.013	0.001	0.005	0.004
Ratio of Egg Length to Width (RELEW)	1.445	0.095	1.324	1.266	1.444	1.481

*All measurements in mm.

as well as the oral sucker length and width, also aid in the taxonomic identification of this species.

It is apparent that, on the basis of those variables studied in this investigation, avian definitive hosts are by far the most suitable ones for *P. minimum*. Internal organs are best developed with respect to size, and their position remains more constant than do those of worms reared in other vertebrate classes. Mammalian definitive hosts also serve as "normal hosts" to a lesser degree, for the extent of the vitellaria and the nature of the oral sucker are somewhat

TABLE 7. Comparison of body and egg measurements of reported species of *Posthodiplostomum* with those reported in this study.*

Species of *Posthodiplostomum*	Body Length		Body Width		Egg Length		Egg Width	
	Min.	Max.	Min.	Max.	Min.	Max.	Min.	Max.
P. australe (Dubois 1937)	0.766	1.150	—	—	0.080	0.091	0.052	0.062
P. bi-ellipticum (Dubois 1958)	1.190	1.230	0.530	0.560	0.078	0.078	0.056	0.056
P. botauri (Vidyarthi 1938)	1.200	1.562	0.256	0.720	0.080	0.080	0.064	0.064
P. boydae (Dubois 1969)	0.990	1.140	0.120	0.180	0.097	0.097	0.058	0.058
P. brevicaudatum (Nordmann 1832, Wisniewski 1958)	1.300	1.920	—	—	0.090	0.110	0.050	0.065
P. cheni (Yang 1959) Odening 1962	1.269	1.735	0.268	0.454	—	—	—	—
P. cuticola (V. Nordmann 1932, Dubois 1936)	0.670	2.310	0.220	0.920	0.073	0.110	0.051	0.088
P. grande (Diesing 1850) Dubois 1936	1.620	2.250	0.250	1.830	0.070	0.086	0.045	0.055
P. grayi (Verma 1936) Dubois 1938	0.830	1.077	0.210	0.390	0.070	0.093	0.042	0.074
P. huesingi Odening, 1962	1.080	2.600	0.300	1.600	0.073	0.110	0.051	0.080
P. impraeputiatum (Dubois 1934) Dubois 1936	1.200	2.110	0.160	0.430	0.092	0.103	0.055	0.065
P. larai (Refuerzo et Garcia 1937)	0.810	1.280	—	—	0.070	0.081	0.053	0.074
P. macrocotyle Dubois, 1937	0.890	1.200	0.200	0.290	0.077	0.089	0.050	0.057
P. microsicya Dubois, 1936	1.200	1.990	0.190	0.290	0.060	0.072	0.038	0.045
P. milui Fotedar et Reina 1965	—	—	—	—	—	—	—	—
P. nanum Dubois, 1937	0.410	0.950	0.090	0.610	0.062	0.076	0.042	0.048
P. oblongum Dubois, 1937	2.340	2.700	0.300	0.540	—	—	—	—
P. opisthosilya Dubois, 1969	0.910	1.160	—	—	0.092	0.096	0.057	0.070
P. podicipitis (Yamaguti 1939)	0.660	1.100	0.200	0.310	0.090	0.093	0.057	0.066
P. prosostomum (Dubois et Rausch) (Dubois 1952 comb. emend.)	2.300	2.530	0.450	0.500	0.082	0.090	0.052	0.058
P. scardinii (Shulman in Dubinin 1952)	—	—	—	—	—	—	—	—
P. suni N. T. Lee, 1964	1.840	1.890	0.301	0.301	0.073	0.073	0.053	0.053
P. minimum (MacCallum 1921)	0.840	1.750	0.160	0.600	0.073	0.091	0.048	0.064
This study	Mean		Mean		Mean		Mean	
P. minimum (Amphibia)	0.517		0.269		0.039		0.028	
P. minimum (Reptilia)	0.435		0.230		0.025		0.020	
P. minimum (Aves)	0.614		0.288		0.084		0.058	
P. minimum (Mammalia)	0.589		0.296		0.085		0.057	

*All measurements in mm.

more variable than in avian hosts. Poikilothermic hosts demonstrate marked variation and abnormal development. Especially among the Reptilia are extreme effects noticeable in developing worms, as evidenced by great reduction in body and organ size when compared with individuals reared in other host classes.

Throughout the literature, extensive synonymy exists for many species of *Posthodiplostomum*. Neither Dubois (1968, 1970) nor Yamaguti (1971) agree as to the number of valid species of this genus. As indicated by this investigation, few characters can be effectively utilized in separating adults of *P. minimum* reared in a great variety of poikilothermic and homiothermic hosts. Experimentally developed *P. minimum* from one or more classes of vertebrate hosts demonstrate such a wide degree of morphological variation that one doubts the validity of the number of species currently placed in the genus *Posthodiplostomum* as well as related genera in this strigeoid group. Certain characters such as body shape, ovary position relative to the testes, extent of vitellaria, relative size of fore- and hindbody, oral sucker shape, and host specificity have been and continue to be used in separating genera of the Diplostomini.

Even if one accepts *Posthodiplostomum* as a valid genus isolated morphologically and genetically from other related genera, the problem of speciation within the genus is even more confusing. Characters used by Dubois (1968, 1970) and Yamaguti (1971) (such as "testes tandem," "anterior testis oval," "posterior testis larger than the anterior testis") appear to be of little value, for this study has shown that host influences upon the adult *P. minimum* render such characters much too "plastic" to be of taxonomic importance. Because of inconsistencies in published accounts of egg sizes and descriptions of the 23 species of *Posthodiplostomum*, it is difficult to make a comparative analysis of them in relation to experimental results derived from this investigation. However, four variables (body length, body width, egg length, and egg width) have been compared (Table 7). Examination of data in this table makes it apparent that several reported species of *Posthodiplostomum* are probably not valid because of the considerable overlap in measurements of these structural features.

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A SURVEY OF BREEDING AND MIGRATORY BIRDS SOUTHWEST OF FARMINGTON, NEW MEXICO

Duane A. Tolle[1]

Abstract.— The relative abundance and habitat affinities of breeding and migratory waterfowl were documented for a 16,556 ha (40,880 acre) area of the Navajo Indian Reservation, San Juan County, New Mexico. The objective of the 1973-1974 study was to obtain baseline data for use as part of an environmental assessment for coal gasification plants and an associated strip mine proposed for an area not previously described in ornithological journals.

Roadside breeding-bird surveys resulted in the observation of 26 species of birds, of which the horned lark was most abundant. Additional breeding-bird observations were made during afternoon reconnaissance surveys around stock ponds and arroyos, and by a helicopter survey of cliff-nesting raptors. Nine of 30 raptor nests located were active.

Migratory waterfowl surveys were made in September and November at four stock ponds and a marsh on the study area. Peak waterfowl numbers were present in September, when teal and shovelers were the most abundant species.

The importance of stock ponds to breeding and migratory birds and the significance of cliffs to nesting raptors were discussed. Details of observations made for five species of birds designated "threatened" or "status undetermined" were presented.

Avifauna of a 16,556 ha (40,880 acre) area (hereafter called the study area) located in San Juan County, New Mexico, about 48.3 km (30 miles) southwest of the city of Farmington were studied during four- to seven-day periods in mid-November 1973 and late February, early June, late September, and mid-November 1974. This overgrazed grassland ecosystem is located in the Navajo Indian Reservation bordering the Chaco River at an elevation of about 1615 m (5300 ft). It is intersected by arroyos which provide a maximum relief of about 122 m (400 ft).

The climate of the study area is arid, with an average of 16.8 cm (6.6 inches) of precipitation per year. The period from July to October normally accounts for half of this precipitation.

The study area includes plants and animals typical of both the grassland and basin sagebrush biociations (Kendeigh 1961). Although vegetation is sparse, it includes grasses, forbes, and low-growing shrubs. A few trees and larger shrubs are located in the arroyos and near ponds. The vegetation has been heavily grazed by livestock, including sheep, cows, horses, and goats. Plants requiring more water are located at the small, man-made stock ponds scattered over the area.

The objective of this study was to document relative abundance and habitat affinities of species of breeding birds and migratory waterfowl, using an area not previously described in ornithological journals, where coal gasification plants and an associated strip mine are planned. These two general groups of birds were considered to be the most likely to be affected by this major industrial development. The resultant baseline data on avifauna of the area was used as part of an environmental impact report.

A substantial number of ducks are present in the San Juan River Valley during the migratory season, due in part to the concentrated production of food crops in this valley (Huey 1967). Bellrose (1971) considers the San Juan River Valley to be a major (nationwide) waterfowl concentration area. Undoubtedly, the attractiveness of the San

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Juan River Valley influences waterfowl use of ponds on the study area.

The San Juan River is part of the Upper Colorado River Basin, which is known as an important migratory route for waterfowl and shorebirds, as well as smaller passerine birds. The Upper Basin has been the site of continued development of aquatic habitat in the form of lakes and reservoirs. This has materially changed the status of waterfowl and shorebirds thoughout the entire area (Hayward, 1967). Morgan Lake and Navajo Reservoir are examples of the water bodies which have recently been created in the San Juan River area of New Mexico.

METHODS

Avifauna of the study area were surveyed by three methods during the breeding season and by two additional methods during the migratory seasons. All common names of birds are reported in the form designated by the Fifth AOU checklist (Wetmore 1957) and the twenty-third supplement (Eisenmann, 1973) (See Appendix I.).

BREEDING BIRD SURVEY METHODS.— *Roadside surveys:* Breeding birds were surveyed during 1 to 7 June 1974 by the following three methods: (1) roadside surveys, (2) reconnaissance surveys along stock pond arroyos, and (3) a helicopter survey of cliff-nesting raptors. The roadside survey developed by the U.S. Department of the Interior (1973a) was conducted on four mornings to obtain an index of abundance of breeding birds. The only variance from the standard operating procedure was the seven-hour period required for completion of the survey. Four and one-half hours are normally allotted to reach the end of a 40.2 km (25 mile) route, with three-minute stops made 0.8 km (0.5 miles) apart to count all birds within a 0.4 km (0.25 mile) radius. On this study area, the additional time was necessary due to the rough roads and backtracking required to reach a representative portion of the area.

All four roadside surveys were run on mornings without precipitation or fog. Wind speed was less than Beaufort 3 (8–12 mph) during all survey periods except for the finish of the 2 and 3 June surveys.

Midafternoon reconnaissance surveys: Afternoon surveys were conducted at five stock ponds (only one had water during the survey period) and their adjacent vegetation, plus five arroyos. Walking surveys were made by a party of two observers for a total of eight hours after each of the four roadside surveys, and during the afternoon of 5 June. A special effort was made to locate nests.

Helicopter survey of raptor nests: Four hours were spent searching for cliff nests of large raptors from a Bell B-1 helicopter on 4 June 1974. A total of 112.7 km (70 miles) of suitable cliff-nesting areas were searched, using the helicopter flight patterns suggested by White and Sherrod (1973) to avoid disturbance of adult and nestling raptors. The flight was made at a time when most of the raptors in the area had finished incubation, but before the majority of the nestlings had fledged. During this period the adult raptors are least likely to desert the nest.

One of the two observers plotted nest locations on topographic maps. The number and description of eggs or nestlings, plus nest materials, diameter, and height were recorded for identification of inactive nests or nests where adults were absent. Photos were taken of nearly all of the nests.

MIGRATORY-BIRD SURVEY METHODS.— *Waterfowl surveys:* Waterfowl surveys were made during the following four periods: (1) 13-16 November 1973, (2) 20-24 February 1974, (3) 22-25 September 1974, and (4) 11-14 November 1974. The November and February survey periods were chosen to coincide with the peak period of both waterfowl numbers and variety of species migrating through San Juan County. The September period was chosen to coincide with peak populations of early migrants (J. L. Sands, pers. comm.).

Five waterfowl observation sites were selected on the study area. Of these five sites, four were at man-made stock ponds created by damming arroyos, and one was at a marsh created by overflow from a spring-fed stock pond. When any one of the ponds was dry or frozen during a survey period, no counts were made. Since all ponds were frozen in February 1974, no waterfowl surveys were made. During all other survey periods, 0.5-hour observation periods were conducted at each of the sites.

General observation of non-waterfowl birds: Non-waterfowl bird species were also recorded during each of the four waterfowl survey periods listed above. An accurate census during these periods was not possible, due to the nonterritorial, flocking behavior of most nonbreeding birds. However, the total number of each species observed was recorded. These data were used to prepare tables of the relative frequency of observation of all nonwaterfowl species. Small birds not associated with the playas or marsh were likely missed. A special effort was made to record all raptors observed while driving between survey sites.

SURVEY RESULTS

RELATIVE ABUNDANCE AND DISTRIBUTION OF BREEDING BIRDS.— *Species observed along roads:* Twenty-six species of birds were heard or observed during 200 three-minute stops made over a four-day period (Table 1). The most abundant species was the Horned Lark, followed by the Mourning Dove and Black-throated Sparrow. The number of stops where a species was observed is an indication of how widely distributed it is over the survey area. The commonness of the Horned Lark probably resulted from the fact that the majority of the study area is relatively flat, mesa habitat with short vegetation which is the preferred habitat for the Horned Lark (Ligon 1961, Fautin 1946).

Species of birds observed at the only marsh on the area were considerably different from birds seen at other survey stops. Nine species of birds were recorded only at a marsh created by overflow from a spring-fed stock pond. These nine species recorded during roadside surveys included the Great Egret, Mallard, Pintail, Green-winged Teal, Cinnamon Teal, Killdeer, Spotted Sandpiper, Tree Swallow, and Brown-headed Cowbird. Also, the following five-bird species were seen at this marsh after the three-minute survey period was over: Savannah Sparrow, Hummingbird (spp. undetermined), American Coot, Western Meadowlark, and Rough-winged Swallow. Observations of all of the above 14 species were restricted to the overflow marsh.

Species observed in arroyos below ponds: Midafternoon reconnaissance surveys around stock ponds and along arroyos resulted in the observation of 21 species of birds (Table 2). Although the time of day prevented an accurate census of the avifauna, a rough estimate of relative abundance between species indicated that the mourning dove, horned lark, and house finch were more abundant around stock ponds and arroyos than other bird species.

Very few nests were located during midafternoon surveys, in spite of a careful search of the vegetation by two observers during eight hours of survey. This searching resulted in the location of active nests of the four following species: Red-tailed Hawk, Ferruginous Hawk, Great Horned Owl, and Cliff Swallow. The Red-tailed Hawk and Cliff Swallow nests were located in cliffs along the Chaco River. Two inactive nests believed to be House Finch nests were located at one of the dry stock pond sites.

Cliff-nesting raptors: Thirty large raptor nests were located during the helicopter survey (Table 3). Nine of these nests were active (Table 4), with the majority of the occupants either Golden Eagles (two nests), Great Horned Owls (two nests), or Red-tailed Hawks (two nests). The Ferruginous Hawk, Prairie Falcon, and Common Raven were recorded at only one nest per species. One of the Golden Eagle nests may have been abandoned, since only one egg and a rock were observed in the nest, and no adult eagle was seen near the nest.

Only four of the six species of raptors had successfully raised young by the survey date (Table 4). Nestling or fledgling Great Horned Owls, Red-tailed Hawks, Ferruginous Hawks, and Common Ravens were observed.

During the helicopter search for nests, a record was kept of all large birds (Table 5). In addition to the six cliff-nesting raptors, eight Mourning Doves, a Burrowing Owl, and two Common Nighthawks were observed during the four-hour flight. The Common Nighthawk was not seen during any of the other surveys; however, no evening surveys were conducted.

Relative abundance of migratory birds.— *Waterfowl at stock ponds:* Ten species of waterfowl were observed during the three survey periods (Table 6). The greatest variety (6) of species were recorded during the November 1973 survey period, but by far the greatest number (268) of individuals were seen during the September 1974 survey period. This large number of individuals was due mainly to the presence of Blue-winged and Cinnamon Teal. These two species of teal and the Northern Shoveler normally migrate south before November in

Table 1. Summary of roadside breeding-bird survey on the study area, June 1974[a].

	Daily Totals				Four-Day Totals	
Common Name	1	2	3	6	Total Individuals	Stops per Species[b]
Horned Lark	77	71	98	74	320	121
Mourning Dove	17	27	18	17	79	53
Black-throated Sparrow	6	23	8	7	44	27
Rock Wren	7	6	15	2	30	25
House Finch	2	14	7	7	30	20
Loggerhead Shrike[c]	3	7	7	8	25	8
Mockingbird	4	3	11	4	22	17
Red-winged Blackbird	4	4	5	7	20	4
Say's Phoebe	3	6	3	3	15	13
Cinnamon Teal	6	2	–	–	8	4
Common Raven	1	2	3	1	7	2
Killdeer	1	4	2	–	7	6
Brown-headed Cowbird	–	–	3	4	7	2
Green-winged Teal	–	1	2	1	4	3
Ferruginous Hawk	–	–	–	3	3	2
Spotted Sandpiper	–	–	3	–	3	1
Mountain Plover[c]	–	1	1	–	2	2
Mallard	–	–	2	–	2	1
Lark Sparrow	2	–	–	–	2	1
Great Egret[d]	–	1	–	–	1	1
Pintail[d]	–	–	–	1	1	1
Golden Eagle	–	–	1	–	1	1
American Kestrel	–	–	–	1	1	1
Burrowing Owl	–	–	1	–	1	1
Empidonax Flycatcher	–	1	–	–	1	1
Tree Swallow	1	–	–	–	1	1
Totals	134	173	190	140	637	
Average Ind./Stop	2.68	3.46	3.80	2.80	3.18	

[a] Fifty three-minute stops were made at 0.8 km (0.5-mile) intervals beginning at 0.5 hour before sunrise on 1, 2, 3, and 6 June 1974. The route was reversed on two days.

[b] Indicates the number of stops, out of a possible 200, when one or more individuals of a species were observed.

[c] Eggs, nestlings, or fledglings observed.

[d] Probably a late spring migrant.

New Mexico (Chattin 1964, Ligon 1961).

Most of the Blue-winged and Cinnamon Teal observations were lumped together because the eclipse molt made positive field identification difficult during September. Female Blue-winged and Cinnamon Teal are inseparable through binoculars all year long.

General observations of nonwaterfowl birds: As expected, the September 1974 survey resulted in observation of the greatest number (32) of nonwaterfowl species out of the four waterfowl survey periods (Table 7). Three-fourths of these species were either shorebirds or passerines. Since the bulk of the shore and passerine bird migration takes place in late April and May and again in late August through early October (Hayward 1967), the September survey period was the most likely to include species in these two large families.

TABLE 2. General reconnaissance survey around stock ponds and along arroyos in the study area, June 1974[a].

Common Name	Frequency of Observations[b]
Red-tailed Hawk[c]	U
Ferruginous Hawk[c]	R
Killdeer	R
Mourning Dove	A
Great Horned Owl[c]	R
Burrowing Owl	R
Western Kingbird	R
Ash-throated Flycatcher	R
Say's Phoebe	C
Empidonax Flycatcher	R
Western Wood Pewee	R
Horned Lark	A
Cliff Swallow[c]	R
Common Raven	U
Rock Wren	U
Mockingbird	U
Northern Oriole	R
Brown-headed Cowbird	R
Blue Grosbeak	R
House Finch	A
Black-throated Sparrow	C

[a] Represents eight hours of midafternoon walking surveys by two observers on 1, 2, 3, 5, and 6 June 1974. Includes surveys at five stock ponds (only one pond had water), and five arroyos (including the dry Chaco River) on the study area.

[b] The approximate number of birds observed are indicated as follows: A = Abundant, 20+; C = Common, 8-19; U = Uncommon, 3-7; and R = Rare, 1-2.

[c] Adult in nest, eggs, nestlings, or fledglings observed.

The fewest (12) species of nonwaterfowl birds were recorded during the February 1974 survey period, when most migrants are still on their wintering grounds. The total bird species seen during each November survey (1973 and 1974) was intermediate in number between species lists for the September and February surveys.

The most frequently observed species during all four survey periods was the Horned Lark. This permanent resident of San Juan County (Hubbard, 1970) was considered abundant during all survey periods except November 1974, when it was considered common relative to other birds observed (Table 7).

Four nonwaterfowl species were observed during seasons not previously recorded by Hubbard (1970) and/or Alan P. Nelson (unpubl. county checklist). These species included one Black-throated Sparrow observed during November 1973, one Swainson's Hawk and 53 Sage Sparrows observed during February 1974, and four Pectoral Sandpipers observed during September 1974.

DISCUSSION

IMPORTANCE OF STOCK PONDS TO DESERT AVIFAUNA.— *Breeding birds:* Some desert birds seen on the study area are dependent on drinking water from the 10 temporary and 4 permanent ponds on the area. In June, 1974, the unusually dry weather reduced the normally "permanent" ponds to only 2. This reduced water supply was undoubtedly a limiting factor for the granivorous birds. Smyth and Coulombe (1971) observed that all of the birds which drank regularly at a desert spring in California were granivorous; three of these species of birds (Mourning Dove, House Finch, and Black-throated Sparrow) were also seen on the study area. Another granivorous bird which requires water every day is the Scaled Quail (Sprunt and Zim 1961). Although the House Finch and Black-throated Sparrow are grain eaters, they may be able to live without drinking when succulent vegetation or insects are available (Smyth and Bartholomew 1966). The Mourning Dove, however, needs water to drink at least once a day (Sprunt and Zim 1961). This may account for the groups of 5 to 10 mourning doves recorded every day at the overflow pond.

Insectivorous, carnivorous, or frugivorous birds were observed to drink very little or not at all at a California desert spring (Smyth and Coulombe 1971). These birds may be limited more by their food resource than by a lack of drinking water. Leopold (1969) suggests that water is no problem for insect feeders and raptors, since the flesh they eat is made up mostly of water. Smyth and Coulombe (1971) listed the following three species which were never seen drinking at the California spring: Ash-throated Flycatcher, Rock Wren, and Loggerhead Shrike. They also listed the Say's Phoebe and Mockingbird as drinking infrequently. All of the above five species were observed

TABLE 3. Helicopter survey of raptor nests on cliffs in the study area, 4 June 1974[a].

Common Name	Nest Number	Nest Diameter (Ft.)	Nest Height Above Ground (Est. in Ft.)	Nest Materials
Great Horned Owl	1	2 (scrape)	30	None (scrape)
?	2	?	40	Sticks
Golden Eagle	3	4-6	150	Twigs + ?
Golden Eagle?	4	4-6	150	Twigs + ?
Golden Eagle?	5	4-6	100	Twigs + ?
Golden Eagle?	6	4	100	Twigs, rock
?	7	3	50	Sticks
Red-tailed Hawk	8	2	50	Sticks and grass
?	9	?	30	Sticks
?	10	?	50	Sticks
?	11	?	50	Sticks
Golden Eagle?	12	?	15	Sticks
Prairie Falcon	13	1.5 (scrape)	40	None (scrape)
?	14	?	—	Sticks
Common Raven	15	2	40	Sticks
Common Raven?	16	2.5	55	Sticks
Common Raven?	17	2.5	55	Sticks
?	18	3	55	Sticks and grass
?	19	3	60	Sticks
?	20	2	70	Sticks
?	21	2.5	60	Sticks
Golden Eagle?	22	3.5	80	Sticks
Ferruginous Hawk?	23	4	50	Sticks, grass, and Yucca stems
Red-tailed Hawk	24	2	40	Sticks (1 rabbit leg)
Falcon?	25	scrape	30	None (scrape)
Golden Eagle?	26	3-5	40	Sticks
Falcon?	27	scrape	50	None (scrape)
Ferruginous Hawk	28[b]	3	0 (on brow of 15' hill)	Sticks, grass, and Yucca stems
?	29	2	40	Sticks (in crevice)
Great Horned Owl	30	scrape	45	None (scrape)

[a] Flying time was four hours in a Bell B-1 helicopter. Two men made observations.

[b] Discovered in low rolling hill area from observation of adults during roadside surveys.

on the study area, and none of them are considered granivorous (Martin et al. 1961). The ability to obtain water through their food may account for the relative abundance of these birds (excluding the Ash-throated Flycatcher) in the roadside survey (Table 1).

The overflow pond which is adjacent to a spring-fed stock pond had the greatest bird diversity of any area of comparable size on the study area. Thirteen species of birds were seen during the June survey only at this location. These species alone represent more than one-quarter of the breeding species recorded. The overflow pond is the only pond with emergent aquatic vegetation on the mine lease, and thus is the only habitat suitable for breeding waterfowl. The four species of dabbling ducks observed at the overflow pond (Table 1) were the only waterfowl observed on the mine lease during the June surveys.

Constant disturbance by livestock drinking at the pond may have prevented waterfowl and other birds from nesting, since no nests were located during a search of the vegetation around the pond. Fautin (1946) suggested that disturbance by livestock at a spring in Utah may have prevented birds from nesting in the area. Also, Hensley (1954) suggested that the constant influx of birds coming to water sources in the Sonoran desert of Arizona may have reduced the number of birds nesting around those limited sources of water. The number of birds, particularly Mourning Doves, coming to the overflow pond to drink, may have increased the disturbance caused by livestock, and

TABLE 5. Flying birds observed during helicopter survey of Wesco Mine Lease, 4 June 1974[a].

Common Name	Number Observed
Red-tailed Hawk[b]	2
Golden Eagle[b]	1
Prairie Falcon[b]	1
American Kestrel	4
Mourning Dove	8
Great Horned Owl[b]	1
Burrowing Owl	1
Common Nighthawk	2
Common Raven[b]	4

[a] Flying time was four hours in a Bell B-1 helicopter. Two men made observations.

[b] Eggs, nestlings, or fledglings observed.

TABLE 4. Active raptor nests located during a helicopter survey, 4 June 1974[a].

Common Name	Nest Number	Number and Color of Eggs	Number and Size[b] of Nestlings	Number and Size[b] of Fledglings
Red-tailed Hawk	8	–	2	–
Red-tailed Hawk	24	1 (white w/dark blotches)	–	1 (⅔ Ad.)
Ferruginous Hawk	28[c]	1 (white w/reddish brown spots)	3 (⅓ Ad.)	–
Golden Eagle	3	–	1 or 2 (¼ Ad.; dead)	–
Golden Eagle?	6	1 (white)	–	–
Prairie Falcon	13	2 (light brown w/dark spots)	1 (hatchling dead?)	–
Great Horned Owl	1	–	3 (½ Ad.)	–
Great Horned Owl	30	–	–	1 (⅔ Ad.)
Common Raven	15	–	5 (⅓ Ad.)	–

[a] Numbers correspond to nest descriptions in Table 3.

[b] Fraction of adult (Ad.) size.

[c] Discovered in low rolling hill area during roadside survey.

thus added to the unsuitability of this area for nesting.

Migratory Waterfowl: Edminster (1964) has noted that the stock ponds in the high plains of New Mexico are not only used for nesting and rearing of young waterfowl, but were visited by surprisingly large numbers of waterfowl and shorebirds during migratory periods. Ponds with aquatic plants and/or ponds with shores that are not bare or overgrazed were most heavily used. Also, dugouts or pit-type ponds are less useful to waterfowl than ponds formed by damming arroyos. Since the overflow pond had gradually sloping sides and emergent vegetation, it is not surprising that many more ducks were seen on it than any other stock pond.

An abundant food supply of aquatic insect larvae and mollusks was probably one reason that the overflow pond was heavily used by migrant Blue-winged Teal, Northern Shovelers, and Bufflehead. During the September 1974 survey, teal accounted for 75 percent of all waterfowl recorded on the study area (Table 6), and all but four ducks recorded were observed at the overflow pond. In addition, 15 of the 17 Bufflehead seen on the study area during both November surveys were seen on the overflow pond (Table 6). About one-quarter of the Blue-winged Teal and Northern Shovelers diet and over three quarters of the Bufflehead's diet are aquatic insects and mollusks (Martin et al. 1961).

Table 6. Migratory waterfowl[a] observations at four stock ponds and a marsh on the study area.

	Number of Observations		
Common Name	Nov. 1973	Sept. 1974	Nov. 1974
Mallard	8		1
Gadwall	2		
Pintail		12	
Green-winged Teal	2	20	
Cinnamon Teal		3	
Blue-winged or Cinnamon Teal		198	
Northern Shoveler		35	
Bufflehead	11		6
Ruddy Duck	2		
American Coot	1		
TOTAL	26	268	7

[a] Although coots are not in the waterfowl family (Anatidae), they were counted along with waterfowl.

IMPORTANCE OF CLIFFS TO NESTING RAPTORS.— Cliffs are important as nesting sites for many of the raptors on the study area, because large trees are nearly nonexistent. Eight species of large raptors (hawks, eagles, falcons, owls, and ravens) were observed during the June surveys (Table 7), and five of these raptors were found nesting on cliff ledges (Table 4). In addition, American Kestrels were observed around cliffs, and probably used them as nesting sites. The American Kestrel is a cavity nester (Ligon 1961), which would make its nest difficult to locate by the helicopter survey used in this study. There was evidence of old Ferruginous Hawk nests on cliffs, although the only active nest found in this study was on the ground. Ligon (1961) reported that Prairie Falcons, Great Horned Owls, and Common Ravens prefer to nest on cliff ledges. He also observed that Red-tailed Hawks, Golden Eagles, and American Kestrels normally nest on cliff ledges or in trees. Therefore, the absence of large trees on the study area, and the fact that most of the large raptor nests located on the study area were on cliff ledges suggests that six of the eight raptor species found on the study area are dependent on the cliffs for nesting.

Although cliff ledges are extremely important to many of the raptors nesting on the study area, they do not appear to be a major limiting factor to raptors in this area. Not only were 21 inactive cliff nests located (Tables 3 and 4), but also distance between existing nests was greater than for three other western study areas. Two nests each were located for the Red-tailed Hawk and Great Horned Owl in this study (Table 4). Distances between these nests were 8.1 km (5 miles) for the Red-tailed Hawk and 10.5 km (6.5 miles) for the Great Horned Owl. However, Craighead and Craighead (1969) found that the maximum diameter of nesting ranges for both the above raptors was 2.4 km (1.5 miles) at their semiwilderness study area near Moose, Wyoming. Also, Smith (1969) found that great horned owl nests averaged 1.6 km (1 mile) apart in the Great Basin desert of central western Utah. Maximum and minimum distances between nearest owl nests were 4.8 km (3 miles) and 1.2 km (0.75 miles). In contrast, Hensley (1954) studied the Red-tailed Hawk in the lower Sonoran desert of Arizona and found that the greatest distance between two nests was about 9.7 km (6 miles), while the closest distance was about 4.8 km (3 miles). It appears that nesting distances are greatest in the cold desert of this study area, least in the Wyoming wilderness area and Great Basin desert of Utah, and intermediate in a warm desert habitat.

PEAK WATERFOWL MIGRATION PERIODS.—No set patterns have been established when any one species can be counted on to occur in peak numbers in the San Juan River valley (J. L. Sands, pers. comm.). The peak population of each species migrating through San Juan County depends on weather conditions and brood population. However, some of the species observed during this study appeared to peak during the portion of the season considered normal for that species. Blue-winged Teal, Cinnamon Teal, and Northern Shovelers are considered

TABLE 7. Nonwaterfowl birds observed during four migratory waterfowl surveys[a] on the study area.

	Frequency of Observation[b] during Survey Periods					Frequency of Observation[b] during Survey Periods			
Common Name	1	2	3	4	Common Name	1	2	3	4
Turkey Vulture	R	-	-	-	Common Raven	C	U	U	U
Cooper's Hawk	-	-	R	-	Rock Wren	-	-	R	-
Red-tailed Hawk	R	R	R	U	Sage Thrasher	-	-	R	-
Swainson's Hawk	-	R	-	-	American Robin	-	-	R	-
Rough-legged Hawk	-	R	-	-	Blue-gray Gnatcatcher	-	-	U	-
Ferruginous Hawk	R	-	R	U	Ruby-crowned Kinglet	-	-	R	-
Golden Eagle	-	R	-	R	Loggerhead Shrike	R	R	-	U
Marsh Hawk	-	R	R	R	Yellow-rumped Warbler	-	-	R	-
Prairie Falcon	R	R	R	R	(Audubon's Var.)				
Merlin	R	-	-	-	Wilson's Warbler	-	-	U	-
American Kestrel	R	-	R	-	Western Meadowlark	-	-	-	R
Scaled Quail	C	-	-	-	Yellow-headed Blackbird	-	-	U	-
Killdeer	-	-	U	-	Red-winged Blackbird	R	-	-	R
Pectoral Sandpiper	-	-	R	-	Cassin's Finch	R	-	-	-
American Avocet	-	-	U	R	House Finch	R	R	R	R
Wilson's Phalarope	-	-	R	-	Green-tailed Towhee	-	-	U	-
Mourning Dove	-	-	R	-	Vesper Sparrow	-	-	R	-
Great Horned Owl	R	-	-	R	Black-throated Sparrow	R	-	-	-
Burrowing Owl	-	-	R	-	Sage Sparrow	U	C	R	U
Say's Phoebe	-	-	R	-	Dark-eyed Junco	-	U	-	-
Western Wood Pewee	-	-	R	-	Clay-colored Sparrow	-	-	R	-
Horned Lark	A	A	A	C	Brewer's Sparrow	-	-	U	-
Bank Swallow	-	-	R	-	White-crowned Sparrow	R	-	-	R
Barn Swallow	-	-	R	-	Number of Species	17	12	32	15

[a] Surveys were made during the following four periods: (1) 13-16 November 1973, (2) 20-24 February 1974, (3) 22-25 September 1974, and (4) 11-14 November 1974.

[b] These birds were not censused. Letters indicate frequency of observation during waterfowl surveys. The approximate number of observations are indicated as follows: A = Abundant, 200+; C = Common, 30-199; U = Uncommon, 5-29; R = Rare, 1-4.

early fall migrants (Chattin 1964, Bellrose 1976). These ducks were relatively abundant during the September survey but were absent during the November surveys (Table 6).

The Mallard is hardy, and normally migrates southward late, when it is forced to move south by the fall freeze (Chattin 1964). Since the Mallard is a permanent resident in San Juan County (Hubbard 1970), the fall migration is usually apparent as a steady increase in numbers. In surveys on the study area, Mallards were relatively common only in November of 1973 but were absent in September (Table 6).

Peak waterfowl use of stock ponds on the study area probably occurs during late September due to the preference of early migrants for this habitat type. The normal peak of fall waterfowl migration through San Juan County is in mid-November (J. L. Sands, pers. comm.). However, early migrants like Cinnamon Teal, Blue-winged Teal, and Northern Shovelers prefer to feed in shallow water, and thus make frequent use of small ponds (Sprunt and Zim 1961). On the other hand, ducks such as the Mallard constitute a major portion of the waterfowl migrants present along the San Juan River during November (J. L. Sands, pers. comm.). Because these birds often feed on waste grain (Bellrose 1976), they are attracted to the fields along the river and probably do not utilize desert ponds in San Juan County to the degree that teal and shovelers do. The effect on fall waterfowl migration is that the major wetland areas in San Juan County (along the San Juan River) are heavily used by late-migrating species, and desert ponds (like those on the study area) are primarily used by early-migrating species.

THREATENED OR STATUS UNDETERMINED SPECIES.— Four species of birds observed on the study area during the June breeding bird surveys deserve detailed discussion due to their federal designation as "threatened" (Prairie Falcon) or "status undetermined" (Ferruginous Hawk, Mountain Plover, and Burrowing Owl) (U.S. Department of the Interior 1973b). Two Prairie Falcons were observed in separate locations at the cliffs bordering the Chaco River. A Prairie Falcon nest with eggs was located at one of these sites on a tall rock column (Tables 3 and 4). A pair of Ferruginous Hawks (plus their nest, Tables 3 and 4) and three Mountain Plovers (plus one nest) were located on open mesa habitat, where the vegetation varies from 0.6 m (2 feet) tall to nonexistent and the soil is sandy with some gravel (Tolle, 1976). Four Burrowing Owls were observed at three different Gunnison's prairie dog towns on the mine lease. In addition, a Merlin (which is considered "status undetermined") was seen during migratory surveys in November 1973.

The Ferruginous Hawk nest located on the study area was slightly less than 1.6 km (1 mile) from a Gunnison's prairie dog town. Because the prairie dog is one of this hawk's major food sources (Ligon 1961), the prairie dog town may have influenced the nest location.

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APPENDIX I. Scientific nomenclature of birds observed on the study area.

Common Name[a]	Scientific Name[a]	Common Name[a]	Scientific Name[a]
Great Egret	*Casmerodius albus*	Ash-throated Flycatcher	*Myiarchus cinerascens*
Mallard	*Anas platyrhynchos*	Western Wood Pewee	*Contopus sordidulus*
Gadwall	*Anas strepera*	Horned Lark	*Eremophila alpestris*
Pintail	*Anas acuta*	Tree Swallow	*Iridoprocne bicolor*
Green-winged Teal	*Anas crecca*	Bank Swallow	*Riparia riparia*
Blue-winged Teal	*Anas discors*	Barn Swallow	*Hirundo rustica*
Cinnamon Teal	*Anas cyanoptera*	Cliff Swallow	*Petrochelidon pyrrhonota*
Northern Shoveler	*Anas clypeata*	Common Raven	*Corvus corax*
Bufflehead	*Bucephala albeola*	Rock Wren	*Salpinctes obsoletus*
Ruddy Duck	*Oxyura jamaicensis*	Mockingbird	*Mimus polyglottos*
Turkey Vulture	*Cathartes aura*	Sage Thrasher	*Oreoscoptes montanus*
Cooper's Hawk	*Accipiter cooperii*	American Robin	*Turdus migratorius*
Red-tailed Hawk	*Buteo jamaicensis*	Blue-gray Gnatcatcher	*Polioptila caerulea*
Swainson's Hawk	*Buteo swainsoni*	Ruby-crowned Kinglet	*Regulus calendula*
Rough-legged Hawk	*Buteo lagopus*	Loggerhead Shrike	*Lanius ludovicianus*
Ferruginous Hawk	*Buteo regalis*	Yellow-rumped Warbler	*Dendroica coronata*
Golden Eagle	*Aquila chrysaetos*	Wilson's Warbler	*Wilsonia pusilla*
Marsh Hawk	*Circus cyaneus*	Western Meadowlark	*Sturnella neglecta*
Prairie Falcon	*Falco mexicanus*	Yellow-headed Blackbird	*Xanthocephalus xanthocephalus*
Merlin	*Falco columbarius*		
American Kestrel	*Falco sparverius*	Red-winged Blackbird	*Agelaius phoeniceus*
Scaled Quail	*Callipepla squamata*	Northern Oriole	*Icterus galbula*
American Coot	*Fulica americana*	Brown-headed Cowbird	*Molothrus ater*
Killdeer	*Charadrius vociferus*	Blue Grosbeak	*Guiraca caerulea*
Mountain Plover	*Charadrius montanus*	Cassin's Finch	*Carpodacus cassinii*
Spotted Sandpiper	*Actitis macularia*	House Finch	*Carpodacus mexicanus*
Pectoral Sandpiper	*Calidris melanotos*	Green-tailed Towhee	*Chlorura chlorura*
American Avocet	*Recurvirostra americana*	Vesper Sparrow	*Pooecetes gramineus*
Wilson's Phalarope	*Steganopus tricolor*	Black-throated Sparrow	*Amphispiza bilineata*
Mourning Dove	*Zenaida macroura*	Lark Sparrow	*Chondestes grammacus*
Great Horned Owl	*Bubo virginianus*	Sage Sparrow	*Amphispiza belli*
Burrowing Owl	*Speotyto cunicularia*	Dark-eyed Junco	*Junco hyemalis*
Common Nighthawk	*Chordeiles minor*	Clay-colored Sparrow	*Spizella pallida*
Western Kingbird	*Tyrannus verticalis*	Brewer's Sparrow	*Spizella breweri*
Say's Phoebe	*Sayornis saya*	White-crowned Sparrow	*Zonotrichia leucophrys*

[a] Common and scientific names are from the Fifth AOU Check-list (Wetmore, 1957) with revisions from the 32d Supplement (Eisenmann, 1973).

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A NEW MONOTYPIC GENUS OF CHIGGERS AND FOUR NEW SPECIES OF *QUADRASETA* FROM VENEZUELA (ACARI: TROMBICULIDAE)[1]

M. L. Goff and J. M. Brennan[2]

Abstract.— *Carebareia*, n. gen., and its type-species, *C. johnstoni*, n. sp., are described. The genus *Quadraseta* Brennan, 1970, is redefined and a key to the 11 included species given. Four new species, *Quadraseta tachirensis*, holotype ex *Akodon* sp., *Q. rotstieri*, ex *Proechimys guyannensis*, *Q. mirandae*, holotype ex *Oryzomys albigularis*, and *Q. falconensis*, ex *Sylvilagus floridanus*, are described.

Four new species of *Quadraseta* Brennan, 1970, and a new monotypic genus, all from Venezuela, are described and illustrated below. Hosts are small mammals.

Collections were made under the direction of Dr. Charles O. Handley, Smithsonian Institution, Dr. Vernon J. Tipton, Brigham Young University, and Dr. Conrad E. Yunker, Rocky Mountain Laboratory. Holotypes are in the collection of the U.S. National Museum of Natural History (currently housed at the Bishop Museum, Honolulu, Hawaii) and paratypes are there and in the collection of the Bishop Museum. All measurements are given in micrometers of the holotypes followed in parentheses by the means and extremes of the type series.

Quadraseta Brennan

Quadraseta Brennan, 1970: 1695; Brennan & Reed, 1975: 62.

Type-species.— Euschoengastia pazca Brennan & Jones, 1964: 700.

Diagnosis.— Trombiculine larvae parasitic on small mammals and, occasionally, birds; legs 7-segmented; coxae unisetose; 2-3 genualae I, genuala II and III; tibiala III; subterminala and parasubterminala I; 6 branched setae in basal whorl of tarsus I. Scutum sparsely punctate; subrectangular, with sinuous anterior and posterior margins; 5 setae; sensilla clavate to capitate. Eyes 2/2. Cheliceral blades with tricuspid cap; palpal tarsus with 4B; palpal claw 3-pronged.

Quadraseta tachirensis, n. sp.

Fig. 1

Type data.— Holotype and 7 paratypes from Tachira, San Cristobal, 21-III-1968, ex *Akodon* sp. (RML 53653); 2 paratypes, same data except 15-III-1968, ex *Akodon bogotensis* (RML 55933).

Diagnosis.— Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala B; 3 genualae I; 54 dorsal body setae; 2 pairs of humeral setae; PL>AM>AL; PW/SD = 1.83.

Description of species.— Larvae. *Idiosoma:* Measuring 290 x 235 in engorged specimen. Eyes 2/2, anterior larger, on ocular plate. Two pairs of humeral setae, measuring 44-46; 54 dorsal body setae, measuring 32-40, arranged 6-10-14-10-6-6-2; 2 pairs of sternal setae, anterior 37-40, posterior 28-31; 42 preanal setae, 20-24; 20 postanal setae, 28-33; total body setae 124. *Gnathosoma:* Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala B; chela (27) with tricuspid cap. *Scutum:* Sparsely punctate; anterior margin biconcave, posterior margin biconvex; AM base in line with AL bases; SB anterior to PL bases; PL>AM>AL; sensilla capitate, head with setules; PW/SD =

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1.83. Scutal measurements: AW 47 (48, 47-49); PW 66 (66, 62-69); SB 22 (19, 17-22); ASB 22 (22, 20-23); PSB 14 (14, 12-16); AP 25 (25, 24-27); AM 25 (29, 25-32); AL 23 (26, 23-30); PL 41 (45, 41-48); sens. 34 x 15 (35, 33-37 x 14-15). *Legs:* All 7-segmented terminating in a pair of claws and a claw-like empodium. IP = 670-710. *Leg I:* 225-238; coxa with 1 branched seta (1B); trochanter 1B; basifemur 1B; telofemur 5B; genu 4B, 3 genualae, microgenuala; tibia 8B, 2 tibialae, microtibiala; tarsus (56 x 21) 19B, tarsala (14-15), microtarsala, subterminala, parasubterminala, pretarsala. *Leg II:* 205-220; coxa 1B; trochanter 1B; basifemur 2B; telofemur 4B; genu 3B, genuala; tibia 6B, 2 tibialae; tarsus (50 x 19) 14B, tarsala (12-14), microtarsala, pretarsala. *Leg III:* 240-255; coxa 1B; trochanter 1B; basifemur 2B; telofemur 3B; genu 3B, genuala; tibia 6B, tibiala; tarsus (65 x 16) 15B.

Remarks.— *Quadraseta tachirensis* is similar to *Q. pazca* (Brennan & Jones, 1964) in having galeala B and 3 genualae I, but differs in having eyes on a distinct ocular plate, PW/SD = 1.83 (1.51 in *Q. pazca*), and arrangement of body setae.

Additional specimens examined (40).—

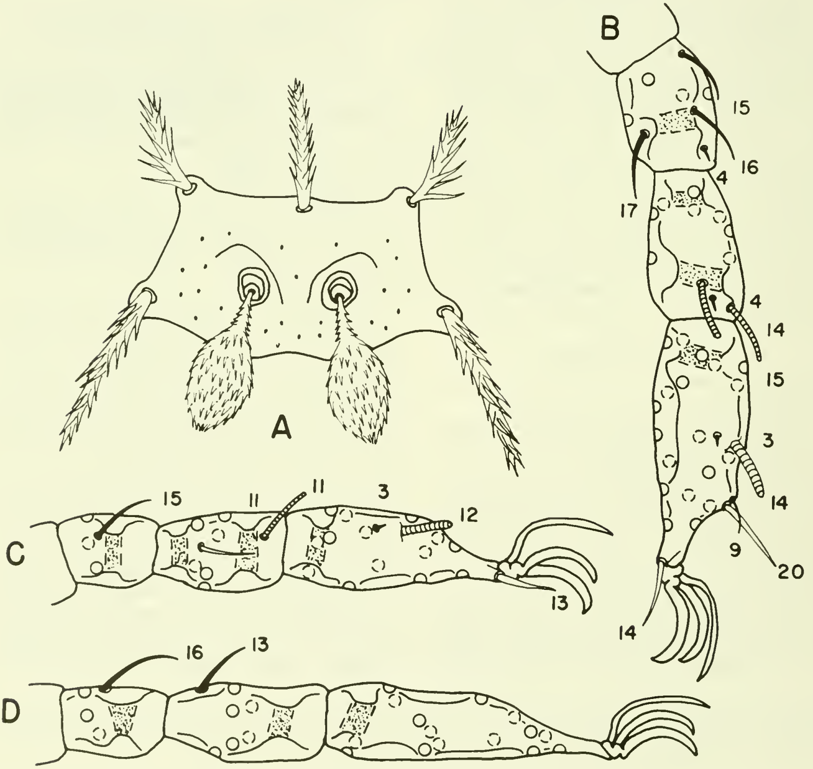

Fig. 1. Larva of *Quadraseta tachirensis:* (a) scutum; (b) leg I distal 3 segments showing specialized setae (measurements in micrometers) and bases of branched setae; (c) leg II, as above; (d) leg III, as above.

Guarico, 6.I.1968, 1 *Zygodontomys* sp. (7). Tachira, San Cristobal, 2-17-III-1968, 2 *Akodon* sp. (20), 1 *Akodon bogotensis* (2), 1 *Oryzomys* sp. (3), 1 *Oryzomys albigularis* (1), 2 *Oryzomys minutus* (6). Yaracuy, W of San Felipe, 8-XII-1967, 1 *Oryzomys capito* (1).

Quadraseta rotstieri, n. sp.

Fig. 2

Type data.— Holotype and 8 paratypes from Falcón, E of Maracaibo, ex *Proechimys guyannensis* (RML 53271), 13-V-1968.

Diagnosis.— Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala N; 2 genualae I, genuala II and III; genu I with 5 branched setae; tibiala III; 58 dorsal body setae, arranged 8-8-10-6-10-4-6-6; sensilla clavate; PW/SD = 1.90-1.97.

Description of species.— Larvae. *Idiosoma:* Measuring 400 x 305 in engorged specimen. Eyes 2/2, of equal size, on ocular plate. Two pairs of humeral setae, measuring 46-48; 58 dorsal body setae, measuring 32-41, arranged 8-8-10-6-10-4-6-6; 2 pairs of sternal setae, 30; 28 preanal setae, 20-26; 30 postanal setae, 30-35; total body setae 124.

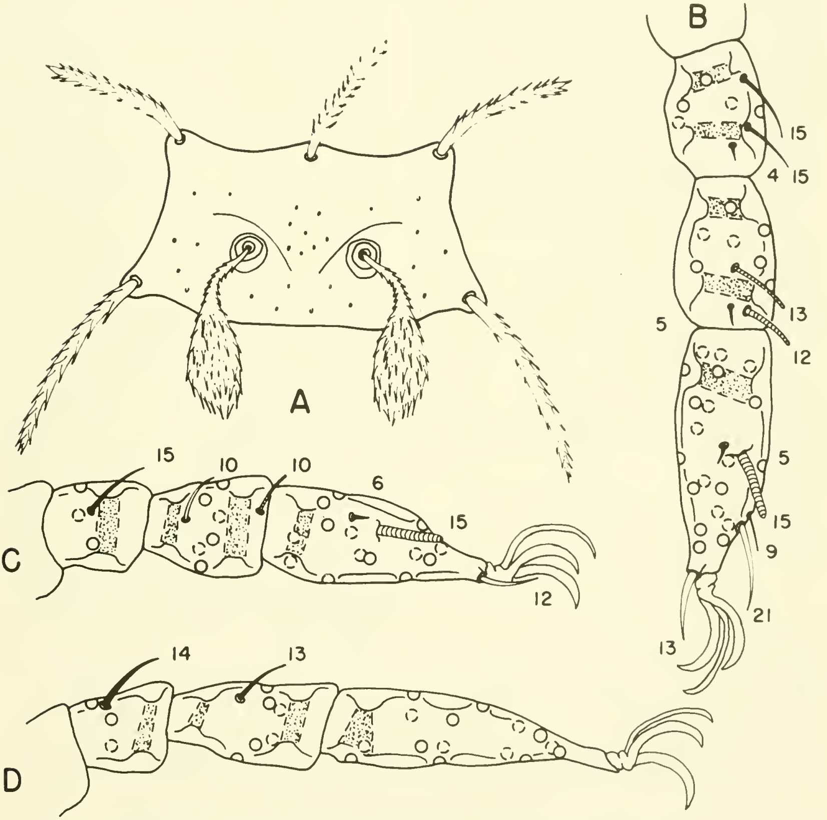

Fig. 2. Larva of *Quadraseta rotstieri:* (a) scutum; (b) leg I distal 3 segments showing specialized setae (measurements in micrometers) and bases of branched setae; (c) leg II, as above; (d) leg III, as above.

Gnathosoma: Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala N; chela (35-38) with tricuspid cap. *Scutum:* Sparsely punctate; anterior margin biconcave, posterior margin biconvex; AM base posterior to AL bases; SB anterior to PL bases; PL>AL>AM; sensilla clavate, head with setules; PW/SD = 1.90-1.97. Scutal measurements: AW 56 (56, 52-59); PW 73 (76, 73-80); SB 22 (24, 22-27); ASB 23 (24, 20-27); PSB 14 (16, 14-17); AP 28 (30, 28-35); AM 36 (36, 33-38); AL 38 (38, 34-40); PL 55 (52, 48-56); sens. missing in holotype (43 x 13, 42-45 x 13). *Legs:* All 7-segmented, terminating in a pair of claws and a clawlike empodium. Onychotrictes absent. IP = 690-717. *Leg I:* 235-245; coxa 1B; trochanter 1B; basifemur 1B; telofemur 5B; genu 5B, 2 genualae, microgenuala; tibia 8B, 2 tibialae, microtibiala; tarsus (57 x 20) 20B, tarsala (15), microtarsala, subterminala, parasubterminala, pretarsala. *Leg II:* 218-220; coxa 1B; trochanter 1B; basifemur 2B; telofemur 4B; genu 3B, genuala; tibia 6B, 2 tibialae; tarsus (51 x 19) 14B; tarsala 15; microtarsala, pretarsala. *Leg III:* 238-252; coxa 1B; trochanter 1B; basifemur 2B; telofemur 3B; genu 3B, genuala; tibia 6B, tibiala; tarsus (67 x 17) 15B.

Remarks.— *Quadraseta rotstieri* is similar to *Q. antillarum* (Brennan, 1967) in having 2 genualae I and 4 humeral setae, but differs in having palpal tibia BBB (BNB in *Q. antillarum*), PL>AL, and 5 branched setae on genu I.

Additional specimens examined (18).— Falcón, E of Maracaibo, 13-15-V-1968, 3 *Akodon urichi* (18).

Quadraseta mirandae, n. sp.

Fig. 3

Type data.— Holotype and 9 paratypes from Miranda, 1 km N of Caracas, Quebrada Chacaito, ex *Oryzomys albigularis* (RML 52518), 18-V-1967.

Diagnosis.— Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala N; 3 genualae I; 68 dorsal body setae; 2 pairs of humeral setae; PL>AM>AL; PW/SD = 1.80.

Description of species.— Larvae. *Idiosoma:* Measuring 290 x 225 in engorged specimen. Eyes 2/2, anterior larger, on ocular plate. Two pairs of humeral setae, measuring 49-55; 68 dorsal body setae, measuring 40-50, arranged 10-6-8-10-10-6-10-6-2; 2 pairs of sternal setae, 34-40; 38 preanal setae, 30-35; 22 postanal setae, 34-42; total body setae 136. *Gnathosoma:* Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala N; chela (37-40) with tricuspid cap. *Scutum:* Sparsely punctate; anterior margin shallowly biconcave; posterior margin shallowly convex; AM base slightly posterior to AL bases; SB anterior to PL bases; PL>AM>AL; sensilla clavate, head with coarse setules; PW/SD = 1.80. Scutal measurements: AW 61 (62, 60-64); PW 80 (81, 73-90); SB 28 (28, 23-31); ASB 29 (28, 26-29); PSB 17 (17, 14-18); AP 38 (37, 34-39); AM 44 (48, 44-52); AL 35 (35, 33-37); PL 55 (60, 55-64); sens. 55 x 13 (50, 47-55 x 12-14). *Legs:* All 7-segmented, terminating in a pair of claws and a clawlike empodium. IP = 883-910. *Leg I:* 300-312; coxa 1B; trochanter 1B; basifemur 1B; telofemur 5B; genu 4B, 3 genualae, microgenuala; tibia 8B, 2 tibialae, microtibiala; tarsus (75 x 22) 19B, tarsala (18-20), microtarsala, subterminala, parasubterminala, pretarsala. *Leg II:* 270-280; coxa 1B; trochanter 1B; basifemur 2B; telofemur 4B; genu 3B, genuala; tibia 6B, tibiala; tarsus (68 x 22) 16B, tarsala (18-20), microtarsala, pretarsala. *Leg III:* 305-317; coxa 1B; trochanter 1B; basifemur 2B; telofemur 3B; genu 3B, genuala; tibia 6B, tibiala; tarsus (82 x 18) 15B.

Remarks.— *Quadraseta mirandae* is similar to *Q. flochi* in having 3 genualae I, clavate sensillae and PL>AL, but differs in having tarsalae I and II longer (18-20, 14 and 15, respectively, in *Q. flochi*), posterior scutal margin evenly convex (biconvex in *Q. flochi*) and longer dorsal body setae (40-50 in *Q. mirandae* and 25-30 in *Q. flochi*).

Additional specimens examined (134).— NW of Orania, 1 *Proechimys guyannensis* (1). Bolívar, E of Caicara, 1 *P. guyannensis* (2). Falcón, E of Mirimire, 2 *Heteromys anomalus* (2), 3 *Monodelphis brevicaudata* (20), 1 *Zygodontomys* sp. (2). Lora, N of El Tocuyo, 1 *Echymys* sp. (1). Miranda, Caracas Country Club, 4 *Didelphis marsupialis* (36); 1 km N of Caracas, Quebrada Chacaito, 1 *H. anomalus* (8), 6 *Oryzomys albigularis* (18). Suere, E of Carupano, 1 *H. anomalus* (11), 1 *M. brevicaudata* (5), 1 *P. guyannensis* (4), 1 *Zygodontomys microtinus* (1). Yaracuy, W of San Felipe, 2 *M. brevicaudata* (8). Zulia, Sierra de Perija, 1 *P. guyannensis* (2), 2 *Proechimys* sp. (3).

Quadraseta falconensis, n. sp.

Fig. 4

Type data.— Holotype and 12 paratypes from Falcón, W of Coro, 17-VII-1968, ex *Sylvilagus floridanus* (RML 53360).

Diagnosis.— Palpal setal formula B/B/BNB/4B; palpal claw 3-pronged; galeala N; 3 genualae I; 34 dorsal body setae; 2 pairs of humeral setae; AL>PL>AM; PW/SD = 1.84.

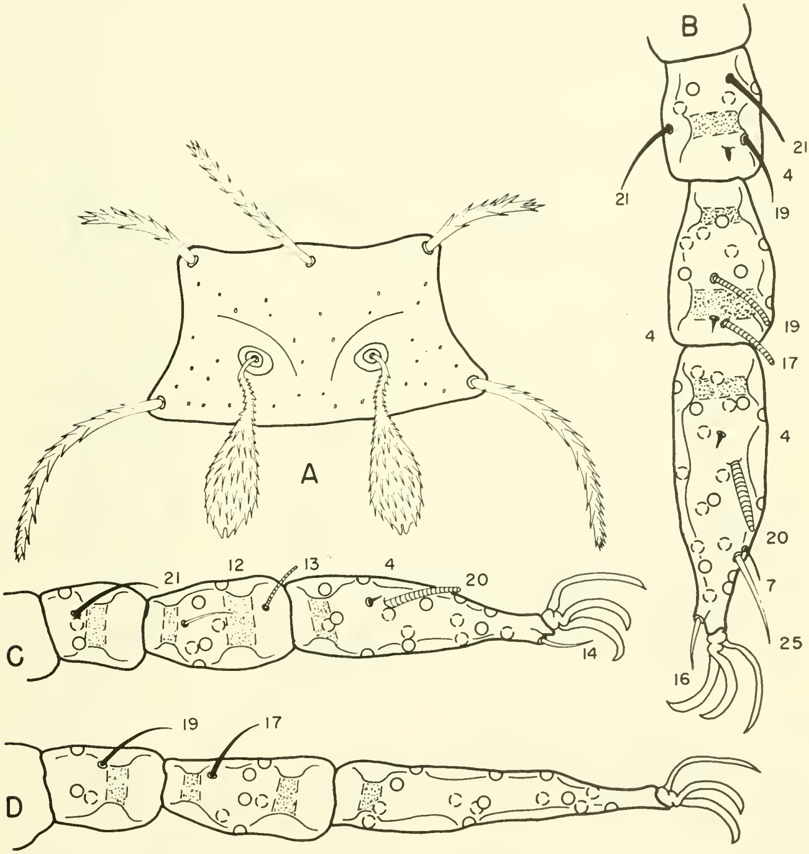

Fig. 3. Larva of *Quadraseta mirandae:* (a) scutum; (b) leg I distal 3 segments showing specialized setae (measurements in micrometers) and bases of branched setae; (c) leg II, as above; (d) leg III, as above.

Description of species.— Larvae. *Idiosoma:* Measuring 430 x 300 in engorged specimen. Eyes 2/2, anterior larger, on ocular plate. Two pairs of humeral setae, measuring 25-28; 34 dorsal body setae, measuring 19-26, arranged 8-10-8-6-2; 2 pairs of sternal setae, 25-27; 18 preanal setae, 15-18; 18 postanal setae, 21-23; total body setae 78. *Gnathosoma:* Palpal setal formula B/B/BNB/4B; palpal claw 3-pronged; galeala N; chela (25) with tricuspid cap. *Scutum:* Sparsely punctate; anterior margin deeply biconcave, posterior margin biconvex; AM base in line with or slightly posterior to AL bases; SB anterior to PL bases; AL>PL>AM; sensilla capitate, head with fine setules; PW/SD = 1.84. Scutal measurements: AW 44 (41, 37-44); PW 61 (57, 52-61); SB 12 (12, 10-13); ASB 22 (22, 20-25); PSB 9 (9, 8-10); AP 26 (25, 22-27); AM 20 (19, 18-20); AL 37 (36, 34-38); PL 32 (31, 28-32); sens. missing in holotype (24, 21-26, head 15 x 16). *Legs:* All 7-segmented, terminating in a pair of claws and a clawlike empodium. IP = 540-560. *Leg I:* 190-195; coxa 1B; trochanter 1B; basifemur 1B; telofemur 5B; genu 4B, 3

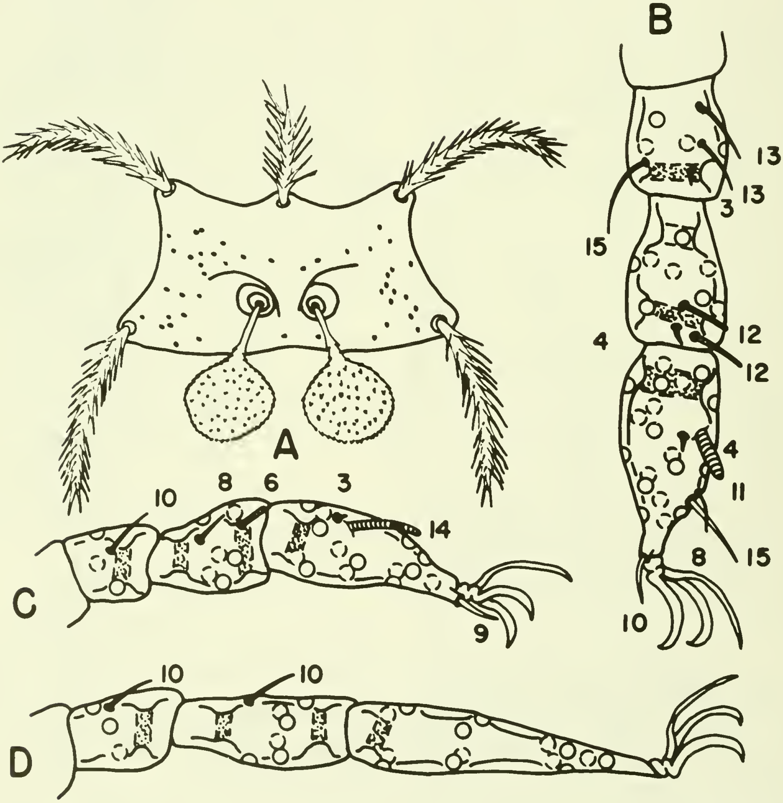

Fig. 4. Larva of *Quadraseta falconensis:* (a) scutum; (b) leg I distal 3 segments showing specialized setae (measurements in micrometers) and bases of branched setae; (c) leg II, as above; (d) leg III, as above.

genualae, microgenuala; tibia 8B, 2 tibialae, microtibiala; tarsus (43 x 17) 19B, tarsala (10-11), microtarsala, subterminala, parasubterminala, pretarsala. *Leg II:* 160; coxa 1B, trochanter 1B; basifemur 2B; telofemur 4B; genu 3B, genuala; tibia 6B, 2 tibialae; tarsus (37 x 15) 14B, tarsala (13-14), microtarsala, pretarsala. *Leg III:* 190-205; coxa 1B; trochanter 1B; basifemur 2B; telofemur 3B; genu 3B, genuala; tibia 6B, tibiala; tarsus (55 x 12) 14B.

Remarks.— *Quadraseta falconensis* shares the character of a nude lateral palpotibial seta with *Q. antillarum* (Brennan, 1967) but differs in having 3 genualae I.

Key to Species of *Quadraseta*

1.	Two genualae I	2
	Three genualae I	5
2(1).	Palpal setal formula B/B/BNB	*antillarum* (Brennan, 1967)
	Palpal setal formula B/B/BBB	3
3(2).	Galeala branched	*azulae* (Brennan & Jones, 1964)
	Galeala nude	4
4(3).	Genu I with 5 branched setae	*rotstieri*, n. sp.
	Genu I with 4 branched setae	*trapezoides* (Brennan & Jones, 1964)
5(1).	Galeala branched	6
	Galeala nude	7
6(5).	$PW/SD>1.75$	*tachirensis*, n. sp.
	$PW/SD<1.55$	*pazca* (Brennan & Jones, 1964)
7(5).	Two humeral setae	*mackenziei* (Yunker & Brennan, 1964)
	Four humeral setae	8
8(7).	Sensilla clavate; more than 60 dorsal body setae	9
	Sensilla capitate, fewer than 50 dorsal body setae	10
9(8).	Tarsala I 18-20; dorsal body setae measuring 40-50	*mirandae*, n. sp.
	Tarsala I 14; dorsal body setae measuring 25-30	*flochi* (Brennan & Jones, 1960)
10(9).	Lateral palpotibial seta nude	*falconensis*, n. sp.
	Lateral palpotibial seta branched	*macarenae* (Brennan & Jones, 1964)

Carebareia, n. gen.

Type-species.— *Carebareia johnstoni* Goff & Brennan, n. sp.

Diagnosis.— Trombiculine larvae. Palpal tarsus 4B; palpal subterminala absent; palpal claw 3-pronged; galeala N; chela with tricuspid cap; sensilla capitate; genuala I, genuala II and III absent; tibiala III; subterminala and parasubterminala I; no mastisetae on leg III.

Remarks.— *Carebareia* is similar to *Quadraseta* Brennan, 1970, but may be separated by having only 1 genuala I (2-3 in *Quadraseta*), lacking genuala II and III and having slightly expanded dorsal body setae. Single genuala I and absence of genuala II and III also serve to separate *Carebareia* from *Aitkenius* Brennan, 1970, *Ectonyx* Brennan, 1960, *Cheladonta* Lipovsky, Crossley & Loomis, 1955, and *Trombewingia* Fonseca, 1955. *Carebareia* is similar to *Kayella* Vercammen-Grandjean, 1960, in having 1 genuala I and lacking genuala II and III, but differs in having both subterminala and parasubterminala I.

Carebareia johnstoni, n. sp.

Fig. 5

Type data.— Holotype and 5 paratypes from Venezuela, Falcón, W of Coro, ex *Marmosa robinsoni* (RML 53544), 25.VII.1968.

Diagnosis.— Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; galeala N; chela with tricuspid cap; eyes 2/2; 1 genuala I; tibiala III; subterminala and parasubterminala I; 54 slightly expanded dorsal body setae; capitate sensilla; PW/SD = 2.10-2.30.

Description of species.— Larvae. *Idiosoma:* Measuring 315 x 220 in partially engorged specimen. Eyes 2/2, anterior larger, on ocular plate. Two pairs of humeral setae, slightly expanded, measuring 26-29; 54 slightly expanded dorsal body setae, measuring 20-22, arranged 8-8-8-6-8-6-6-4; 2 pairs of sternal setae, 28-30; 22 preanal setae, 20-22; 20 postanal setae, similar in form to dorsal body setae, 23; total body setae 104. *Gnathosoma:* Palpal setal formula B/B/BBB/4B; palpal claw 3-pronged; chela (25) with tricuspid cap; galeala N; gnathobase lightly punctate, bearing a pair of branched setae. *Scutum:* Sparsely punctate; anterior margin shallowly biconcave, posterior margin biconvex; AM base in line with AL bases; SB slightly anterior to PL bases; PL>AM>AL; sensilla capitate, head with

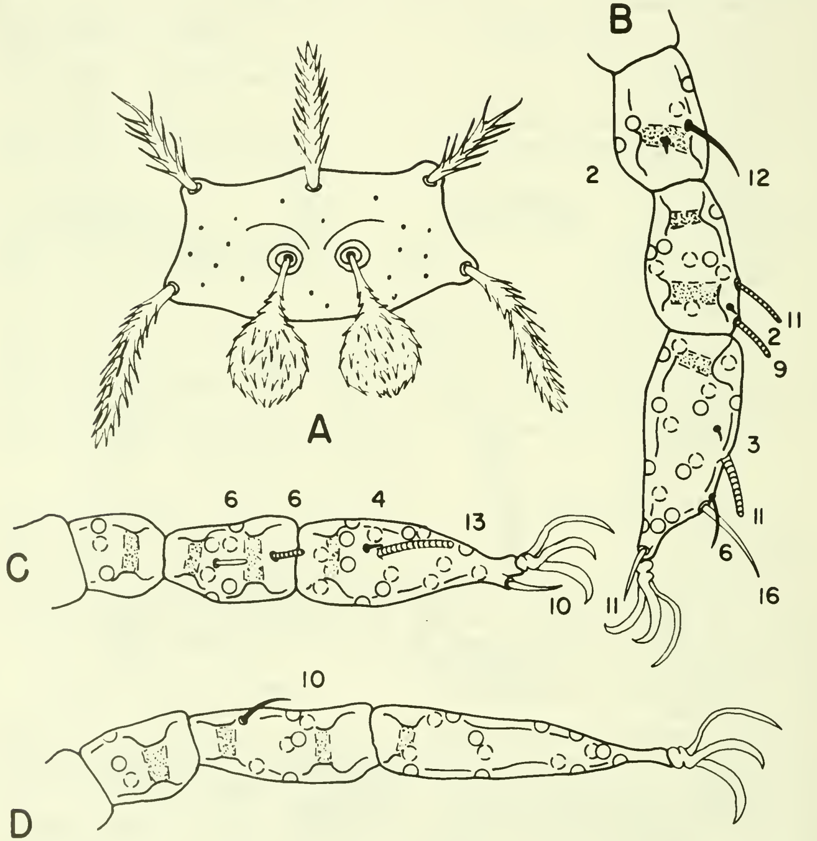

Fig. 5. Larva of *Carebareia johnstoni:* (a) scutum; (b) leg I distal 3 segments showing specialized setae (measurements in micrometers) and bases of branched setae; (c) leg II, as above; (d) leg III, as above.

coarse setules; PW/SD = 2.10-2.30. Scutal measurements: AW 45 (45, 40-50); PW 55 (59, 55-60); SB 10 (15, 10-16); ASB 16 (17, 16-20); PSB 10 (11, 10-12); AP 18 (20, 18-23); AM 26 (27, 26-29); AL 23 (22, 20-24); PL 30 (33, 30-35); sens. 23 x 15 (26 x 15, 23-28 x 15). *Legs:* All 7-segmented, terminating in a pair of claws and a clawlike empodium. Onychotrictes absent. IP = 559-604. *Leg I:* 192-204; coxa with 1 branched seta (1B); trochanter 1B; basifemur 1B; telofemur 5B; genu 4B, genuala, microgenuala; tibia 8B, 2 tibialae, microtibiala; tarsus (47 x 18) 15B; tarsala (10-11), microtarsala, subterminala, parasubterminala, pretarsala. *Leg II:* 170-190; coxa 1B; trochanter 1B; basifemur 2B; telofemur 4B; genu 3B; tibia 6B, 2 tibialae; tarsus (38 x 16) 15B, tarsala (13), microtarsala, pretarsala. *Leg III:* 197-210; coxa 1B; trochanter 1B; basifemur 2B; telofemur 3B; genu 3B; tibia 6B, tibiala; tarsus (52 x 14) 14B.

Remarks.— This species is named in honor of Dr. Donald E. Johnston, Acarology Laboratory, Ohio State University, in recognition of his many significant contributions to acarology.

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A NEW NAME FOR *GALIUM SCABRIUSCULUM* (RUBIACEAE) OF UTAH

Lauramay T. Dempster[1] and Friedrich Ehrendorfer[2]

Abstract.—A new name, *Galium emeryense*, is proposed to substitute for the preempted name *G. scabriusculum.*

The name *Galium scabriusculum* (Ehrend.) Demp. & Ehrend., used in 1965 for a Utah species of the *G. multiflorum* complex, was discovered by us to have been preempted, and therefore invalid. The name was published first as a subspecies of *G. hypotrichium* by Ehrendorfer, later as a variety of *G. coloradoense* by Dempster, and eventually as a species in our joint publication. We have since become aware that a *Galium scabriusculum* was published in 1912: *Galium scabriusculum* (H. Braun) Dalla Torre & Sarnth., Fl. Tirol 6(3): 378 (1912) = *G. nitidulum β scabriusculum* H. Braun ap. Oborny, Fl. Mähren Schlesien 1: 737 (1885!). This is now a synonym of *G. pumilum* Murr., but was validly published as a species. It is therefore necessary to give a new name to the Utah species. The name we propose refers to Emery Co., Utah, which contains the type locality. Full synonymy follows:

Galium emeryense Demp. & Ehrend. nom. nov. *G. hypotrichium* ssp. *scabriusculum* Ehrend., Contr. Dudley Herb. 5: 13. 1956. *G. coloradoense* var. *scabriusculum* Demp., Brittonia 11: 120. 1959. *G. scabriusculum* Demp. & Ehrend., Brittonia 17: 312. 1965. Type: Calf Springs Wash, San Rafael Swell, Emery Co., Utah, *Maguire 18437* (GH. Isotypes CAS, NY, UC, UTC, WTU).

Galium emeryense ssp. *protoscabriusculum* Demp. & Ehrend. comb. nov. *G. scabriusculum* ssp. *protoscabriusculum* Demp. & Ehrend., Brittonia 17: 312. 1965. Type: side canyon ca 1 mile NW of Castle Gate, Carbon Co., Utah, *Ehrendorfer & Stutz 5954* (UC).

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NEW SYNONYMY AND NEW SPECIES OF AMERICAN BARK BEETLES (COLEOPTERA: SCOLYTIDAE), PART VI[1]

Stephen L. Wood[2]

Abstract—. New synonymy of American Scolytidae is proposed as follows: *Corthylus* Erichson (=*Pseudocorthylus* Ferrari), *Hylesinus* Fabricius (=*Leperisinus* Reitter), *Monarthrum* Kirsch (=*Anchonocerus* Eichhoff), *Corthylus spinifer* Schwarz (=*Metacorthylus affinis* Fonseca, *Corthylus affinis* Fonseca), *Cryphalus ruficollis* Hopkins (=*Cryphalus amabilis* Chamberlin, *Cryphalus coloradensis* Wood), *Gnathotrichus retusus* (LeConte) (=*Gnathotrichus alni* Blackman), *Gnathotrichus sulcatus* (LeConte) (=*Gnathotrichus aciculatus* Blackman), *Hypothenemus eruditus* Westwood (=*Hypothenemus germari* Eichhoff, *Stephanoderes mymedon* Eichhoff, *Stephanoderes intersetosus* Eggers), *Hypothenemus seriatus* Eichhoff (=*Stephanoderes nitidulus* Hopkins, *Stephanoderes subopacicollis* Hopkins), *Hypothenemus obscurus* (Fabricius) (=*Stephanoderes asperulus* Eichhoff, *Stephanoderes cassiae* Eichhoff), *Pityophthorus annectens* LeConte (=*Pityophthorus citus* Blackman), *Pityophthorus balsameus* Blackman (=*Pityophthorus patchi* Blackman), *Pityophthorus briscoei* Blackman (=*Pityophthorus mundus* Blackman), *Pityophthorus cariniceps* LeConte (=*Pityophthorus cognatus* Blackman), *Pityophthorus confertus* Swaine (=*Pityophthorus agnatus* Blackman, *Pityophthorus comptus* Blackman), *Pityophthorus confusus* Blandford (=Pityophthorus *bellus* Blackman), *Pityophthorus consimilis* LeConte (=*Pityophthorus nudus* Swaine), *Pityophthorus fuscus* Blackman (=*Pityophthorus smithi* Schedl), *Pityophthorus immanis* Blackman (=*Pityophthorus sulcatus* Bright), *Pityophthorus murrayanae* Blackman (=*Pityophthorus gracilis* Swaine, *Pityophthorus cutleri* Swaine, *Pityophthorus exilis* Swaine, *Pityophthorus depygis* Blackman, *Pityophthorus watsoni* Schedl, *Pityophthorus aurulentis* Bright), *Pityophthorus ornatus* Blackman (=*Pityophthorus limatus* Wood), *Pityophthorus pseudotsugae* Swaine (=*Pityophthorus thatcheri* Bright), *Pityophthorus pullus* Zimmermann (=*Pityophthorus bisulcatus* Eichhoff), *Scolytodes levis* (Blackman) (=*Ctenophorus laevigatus* Chapuis, *Scolytodes chapuisi* Wood). The following species are named as new to science: *Pityophthorus crotonis* (Venezuela), *Scolytodes constrictus*, *S. festus*, *S. praeceps* (Colombia), *S. canaliculus*, *S. contractus*, *S. jucundus*, *S. opacus*, *S. opimus*, *S. serenus*, *S. suturalis*, and *S. varius* (Venezuela).

On the following pages several newly discovered cases of synonymy and 12 species new to science are presented for American Scolytidae. The species new to science represent the genera *Scolytodes* (11) and *Pityophthorus* (1) and were taken in Colombia (3) and Venezuela (9).

New Synonymy

Corthylus Erichson

Corthylus Erichson, 1836, Archiv. Naturgesch. 2(1):64 (Type-species: *Bostrichus compressicornis* Fabricius, subsequent designation by Ferrari, 1867, Die Forst- und Baumsuchtschädlichen Borkenäfer, p. 48)

Pseudocorthylus Ferrari, 1867, Die Forst- und Baumsuchtschädlichen Borkenkäfer, p. 59 (Type-species: *Pseudocorthylus letzneri* Ferrari, subsequent designation by Hopkins, 1914, Proc. U.S. Nat. Mus. 48:128). *New synonymy*

The name *Pseudocorthylus* has appeared in the literature for more than a century in either an uncertain status or as a subgenus of *Corthylus* Erichson. The types of the type-species of both genera were examined. *Pseudocorthylus letzneri* is a normal representative of the genus *Corthylus*. Consequently, *Pseudocorthylus* must be placed in synonymy under the older name as indicated above.

Hylesinus Fabricius

Hylesinus Fabricius, 1801, Syst. Eleuth. 2:390 (Type-species: *Hylesinus crenatus* Fabricius, subsequent designation by Westwood, 1838, Synopsis of the genera of British insects, p. 39)

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[1] Part of the research was sponsored by the National Science Foundation.

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Leperisinus Reitter, 1913, Wiener Ent. Zeit. 32(Beiheft):41 (Type-species: *Bostrichus fraxini* Panzer = *Bostrichus varius* Fabricius, subsequent designation by Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(2):70). *New synonymy*

The genus *Hylesinus* Fabricius contains a diverse group of species from Europe to Australia, with a few species in north Africa and North America. *Leperisinus* was erected for a group of species, found mostly in *Fraxinus*, that differed from *Hylesinus crenatus* Fabricius by the conspicuously scalelike vestiture. After examining most of the species of *Hylesinus* from Europe and Asia and many others from Australia, Indonesia, and the Philippines, it became apparent that the scalelike or hairlike vestiture intergrades to such an extent that it is not a meaningful generic character. If *Hylesinus* were to be divided, the division should come elsewhere in the genus. In the absence of other generic characters, those species previously assigned to *Leperisinus* must be grouped with *H. crenatus* in the genus *Hylesinus*. Thus, *Leperisinus* must be placed in synonymy.

Monarthrum Kirsch

Monarthrum Kirsch, 1866, Berliner Ent. Zeitschr. 10:213 (Type-species: *Monarthrum chapuisi* Kirsch, monobasic)

Anchonocerus Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2)8:431 (Type-species: *Anchonocerus rufipes* Eichhoff, monobasic). *New synonymy*

The holotypes of *Monarthrum chapuisi* Kirsch and *Anchonocerus rufipes* Eichhoff, a long series of the latter species, and more than 70 other species in this genus were examined. It is quite clear that *rufipes* falls well within the generic limits of *Monarthrum*. For this reason the name *Anchonocerus* must be placed in synonymy.

Corthylus spinifer Schwarz

Corthylus spinifer Schwarz, 1891, Proc. Ent. Soc. Washington 2:114 (Syntypes, females; Key West, Florida; U.S. Nat. Mus.)

Metacorthylus affinis Fonseca, 1925, Commissão de Estudio e Debellação da Praga Cafeeira, Pub. 12:3 (Syntypes; Itatiba, São Paulo, Brazil; not located?). *New synonymy*

Corthylus affinis Fonseca, 1927, Rev. Mus. Paul. 15(1):585 (Syntypes; Itatiba, São Paulo, Brazil; not located?). *New synonymy*

Corthylus affinis Fonseca, 1927 is an obvious duplication of the validation of *Metacorthylus affinis* Fonseca, 1925. Four presumed syntypes of Fonseca's species and numerous other specimens from Brazil clearly match the excellent illustrations of this species that accompany the original description. Part of this Brazilian material was compared to the syntypes of *Corthylus spinifer* Schwarz and other material from Florida, Central America, and northern South America. All represent one species. It is very probable that this species reached Florida through commerce from tropical America.

Cryphalus ruficollis Hopkins

Cryphalus ruficollis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:40 (Holotype, female; Alta, Utah; U.S. Nat. Mus.)

Cryphalus amabilis Chamberlin, 1917, Canadian Ent. 49:321 (Lectotype, female; Elk Lake, Oregon; Canadian Nat. Coll., designated by Bright, 1967, Canadian Ent. 99:681). *New synonymy*

Cryphalus ruficollis coloradensis Wood, 1954, Univ. Kansas Sci. Bull. 36(2):1008 Holotype, female; 7 miles N Grand Canyon Nat. Pk., Arizona; Snow Coll., Univ. Kansas). *New synonymy*

The type series of *Cryphalus ruficollis* Hopkins, *C. amabilis* Chamberlin, and *C. ruficollis coloradensis* and more than 300 other specimens were examined and compared. The supposed geographical character gaps observed by me in 1954 have been completely eliminated by subsequent collecting. Therefore, it is necessary to place *amabilis* and *coloradensis* in synonymy under the senior name as indicated above.

Gnathotrichus retusus (LeConte)

Cryphalus retusus LeConte, 1868, Trans. Amer. Ent. Soc. 2:155 (Syntypes; California; Mus. Comp. Zool.)

Gnathotrichus alni Blackman, 1931, J. Washington Acad. Sci. 21:271 (Holotype, female; Hoquiam, Washington; U.S. Nat. Mus.). *New synonymy*

Gnathotrichus alni Blackman was named from a population that breeds in *Alnus* in Washington and Oregon. Except for the host, I have been unable to find characters that distinguish it from *Gnathotrichus retusus* (LeConte), a common species in coniferous hosts in that area. Until biological characters can be found that distinguish *alni* from *retusus,* it should be placed in synonymy as indicated above.

Gnathotrichus sulcatus (LeConte)

Cryphalus sulcatus LeConte 1868, Trans. Amer. Ent. Soc. 2:155 (Holotype, female; middle California; Mus. Comp. Zool.)

Gnathotrichus aciculatus Blackman, 1931, J. Washington Acad. Sci. 21:272 (Holotype, female; Cloudcroft, New Mexico; U.S. Nat. Mus.). *New synonymy*

Gnathotrichus aciculatus Blackman was named from specimens having a deeply, narrowly sulcate elytral declivity. After examining 594 specimens of *G. sulcatus* (LeConte) from throughout its range, it was concluded that the *aciculatus* specimens represent an aberrant form of the species that intergrades completely with normal *sulcatus* specimens. Until biological or other characters can be found that justify recognition of this form, it should be placed in synonymy as indicated above. The type series of both were examined.

Hypothenemus eruditus Westwood

Hypothenemus eruditus Westwood, 1836, Trans. Ent. Soc. London 1(1):34 (Syntypes; England?; some in British Mus. Nat. Hist.)

Stephanoderes germari Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2)8:159 (Syntypes?; Mexico; lost with Hamburg Mus.). *New synonymy*

Stephanoderes myrmedon Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2)8:159 Holotype, female; Colombia; Inst. Roy. Sci. Nat. Belgique, Brussels). *New synonymy*

Stephanoderes intersetosus Eggers, 1928, Archiv. Inst. Biol. Def. Agric. Anim. 1:85 (Lectotype, female; São Paulo, Brazil; U.S. Nat. Mus., designated by Anderson and Anderson, 1971, Smithsonian Contrib. Zool. 94:16). *New synonymy*

The female holotype of *Stephanoderes myrmedon* Eichhoff and the female lectotype of *Stephanoderes intersetosus* Eggers were examined and compared directly to part of my series that was compared to syntypes of *Hypothenemus eruditus* Westwood. It is quite obvious that only one species is represented by this material. The type series of *Stephanoderes germari* Eichhoff was lost with the Hamburg Museum during World War II; consequently, the only means of fixing the identity of this species, other than from the generalized description, is through the examination of specimens compared to the types before they were lost. Five such series were examined and all are conspecific with *eruditus.* For this reason, it was placed in synonymy as indicated above.

Hypothenemus seriatus (Eichhoff)

Stephanoderes seriatus Eichhoff, 1872, Berliner Ent. Zeitschr. 15:133 (Lectotype, female; New Orleans, Louisiana; Inst. Roy. Sci. Nat. Belgique, Brussels, designated by Wood, 1973, Great Basin Nat. 33:177)

Stephanoderes nitidulus Hopkins, 1915, U.S. Dept. Agric. Rept. 99:29 (Holotype, female; Cayamas, Cuba; U.S. Nat. Mus.). *New synonymy*

Stephanoderes subopacicollis Hopkins, 1915, U.S. Dept. Agric. Rept. 99:30 (Holotype, female; Cayamas, Cuba; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Stephanoderes nitidulus* Hopkins and *S. subopacicollis* Hopkins were examined and compared to my material that was previously compared by me to the female lectotype of *Hypothenemus seriatus* (Eichhoff). All of these specimens fall well within the range of variability of *seriatus.*

Hypothenemus obscurus (Fabricius)

Hylesinus obscurus Fabricius, 1801, Syst. Eleuth. 2:395 (Lectotype, female; Essequibo, British Guiana, published as America meridionalis; Copenhagen Mus.)

Stephanoderes asperulus Eichhoff, 1872 (nec. LeConte, 1868), Berliner Ent. Zeitschr. 15:133 (Lectotype, female; *Cassia,* probably from northern South America; Inst. Roy. Sci. Nat., Brussels, present designation). *New synonymy*

Stephanoderes cassiae Eichhoff, 1878, Mém. Soc. Roy. Sci. Liége (2)8:152 (Replacement name for S. *asperulus* Eichhoff). *New synonymy*

Three female syntypes of *Stephanoderes asperulus* Eichhoff are in the Chapuis Collection at the Brussels Museum. The first and third specimens were compared directly by me to my homotypes of *Hypothenemus obscurus* (Fabricius) and are conspecific. The second specimen is of *Hypothenemus seriatus* Eichhoff. I here designate the third syntype, which is in the best condition, as the lectotype of *asperulus* Eichhoff. This action places Eichhoff's name in synonymy under *obscurus* (Fabricius), as indicated above.

Pityophthorus annectens LeConte

Pityophthorus annectens LeConte, 1878, Proc. Amer. Philos. Soc. 17:622 (Lectotype, female; Tampa, Florida; Mus. Comp. Zool., designated by Bright, 1976, Coleopt. Bull. 30:185)

Pityophthorus citus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:137 (Holotype, female; Chiricahua Mts., Arizona; U.S. Nat. Mus.). *New synonymy*

LeConte's series of syntypes of *Pityophthorus annectens* and 148 other specimens from the southeastern United States, Blackman's type series of *P. citus* from Arizona, 16 specimens from near Durango, Durango, Mexico (and several other Mexican specimens), and 22 specimens from Honduras were examined and compared directly. After much study and hesitation, it was concluded that all represent the same species. Consequently, the name *citus* must be placed in synonymy as indicated above.

Pityophthorus balsameus Blackman

Pityophthorus balsameus Blackman, 1922, New York St. Coll. For., Syracuse, Tech. Pub. 16:119 (Holotype, female; Orono, Maine; U.S. Nat. Mus.)

Pityophthorus patchi Blackman, 1922, New York St. Coll. For., Syracuse, Tech. Pub. 16:120 (Holotype, female; Orono, Maine; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Pityophthorus balsameus* Blackman and *P. patchi* Blackman and 108 other specimens were examined and compared. The female frons is variable and intergrades completely between the two named forms. Since *patchi* represents only a minor variant, it is placed in synonymy as indicated above.

Pityophthorus briscoei Blackman

Pityophthorus briscoei Blackman, 1922, New York St. Coll. For., Syracuse, Tech. Pub. 16:123 (Holotype, female; Brunswick, Maine; U.S. Nat. Mus.)

Pityophthorus mundus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:86 (Holotype, female; Littleton, New Hampshire; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Pityophthorus briscoei* Blackman and *P. mundus* Blackman and 145 other specimens of this species were examined. The female frons is unusually variable and includes several forms, with all stages of intermediacy, in addition to those that have been named. Since *mundus* represents no more than a form that is well within the limits of variability for this species, it must be placed in synonymy as indicated above.

Pityophthorus cariniceps LeConte

Pityophthorus cariniceps LeConte, 1876, Proc. Amer. Philos. Soc. 15:353 (Holotype, female; Detroit, Michigan; Mus. Comp. Zool.)

Pityophthorus cognatus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:69 (Holotype, female; Davidson's R., North Carolina; U.S. Nat. Mus.). *New synonymy*

Blackman's series of *Pityophthorus cognatus* was composite. When two series of *P. crassus* Blackman, bearing only collection numbers on their labels, were removed from consideration, it became apparent that the male declivity was exactly the same as one variation found in male *P. cariniceps* LeConte. While the female frons of *cognatus* is usually radically different from *cariniceps*, a few specimens in a very long series form New Brunswick were as in *cognatus*, while others exhibited various stages of intermediacy or one of two forms common in *cariniceps*. In view of the extreme variability in the female frons and male declivity in this species and in the allied species of this group, it appears advisable to place *cognatus* in synonymy as indicated above.

Pityophthorus confertus Swaine

Pityophthorus confertus Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1):27 (Lectotype, female; Adams Lake, British Columbia; Canadian Nat. Coll., designated by Bright, 1967, Canadian Ent. 99:678)

Pityophthorus agnatus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:125 (Holotype, female; Cloudcroft, New Mexico; U.S. Nat. Mus.). *New synonymy*

Pityophthorus comptus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:127 (Holotype, female; Santa Catalina Mts., Arizona; U.S. Nat. Mus.). *New synonymy*

The female holotypes of *Pityophthorus confertus* Swaine, *P. agnatus* Blackman, and *P. comptus* Blackman and more than 3,000 other specimens of this species were examined. Very slight differences in the southern areas of the distribution were noted, represented by *agnatus* and *comptus*, but these are not sufficiently distinct to warrant subspecific recognition. For this reason they were placed in synonymy as indicated above.

Pityophthorus confusus Blandford

Pityophthorus confusus Blandford, 1904, Biol. Centr. Amer., Coleopt. 4(6):237 (Lectotype, female; San Geronimo, Guatemala; British Mus. Nat. Hist., designated by Bright, 1976, Coleopt. Bull. 30:184)

Pityophthorus bellus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:123 (Holotype, female; Monongalia Co., West Virginia; U.S. Nat. Mus.). *New synonymy*

Blandford's syntypes of *Pityophthorus confusus* and 62 other specimens from Mexico, Guatemala, Honduras, and northwestern Nicaragua were examined and compared to the holotype and 306 specimens of *P. bellus* Blackman from the southern United States. They obviously represent the same distinctive species in which I see no basis for recognizing geographical races.

Pityophthorus consimilis LeConte

Pityophthorus consimilis LeConte, 1878, Proc. Amer. Philos. Soc. 17:622 (Lectotype, male; Marquette, Michigan; Mus. Comp. Zool., designated by Bright, 1976, Coleopt. Bull. 30:185)

Pityophthorus nudus Swaine, 1917, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(1):30 (Lectotype, male; Ste. Anne de Bellvue, Quebec; Canadian Nat. Coll., designated by Bright, 1967, Canadian Ent. 99:678). *New synonymy*

The male lectotypes of *Pityophthorus consimilis* LeConte and *P. nudus* Swaine and 382 other specimens were examined. These names were based on the presence or absence of frontal vestiture in the female. Since the character is variable and complete intergradation in series is common, *nudus* must be placed in synonymy as indicated above.

Pityophthorus fuscus Blackman

Pityophthorus fuscus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:32 (Holotype, female; Glacier National Park, Montana; U.S. Nat. Mus.)

Pityophthorus smithi Schedl, 1931, Canadian Ent. 63:163 (Holotype, female; Copper Mountain, British Columbia; Canadian Nat. Coll.). *New synonymy*

The female holotypes of *Pityophthorus fuscus* Blackman and *P. smithi* Schedl and 16 other specimens were examined and compared directly to one another. Only one rare species is represented by this material.

Pityophthorus immanis Blackman

Pityophthorus immanis Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:98 (Holotype, female; Chiricahua Mts., Arizona; U.S. Nat. Mus.)

Pityophthorus sulcatus Bright, 1977, Canadian Ent. 109:528 (Holotype, female; Mt. Lemon, Pima Co., Arizona; Canadian Nat. Coll.). *New synonymy*

The female holotype and seven paratypes of *Pityophthorus immanis* Blackman from the Chiricahua Mts. (one paratype from Flagstaff, Arizona is of *P. crassus* Blackman) and the type series of 86 specimens of *P. sulcatus* Bright were examined. Following a careful study of this material it was concluded that only one species is represented. It is closely allied to *P. abiegnis* Wood.

Pityophthorus murrayanae Blackman

Pityophthorus murrayanae Blackman, 1922, New York St. Coll. For., Syracuse, Tech. Pub. 16:138 (Holotype, female; Grand Lake, Colorado; U.S. Nat. Mus.)

Pityophthorus gracilis Swaine, 1925, Canadian Ent. 57:195 (Holotype, female; Grant Co., Oregon; Candian Nat. Coll.). *New synonymy*

Pityophthorus cutleri Swaine, 1925, Canadian Ent. 57:195 (Holotype, female; Merritt, Midday Valley, British Columbia; Candian Nat. Coll.). *New synonymy*

Pityophthorus exilis Swaine, 1925, Canadian Ent. 57:196 (Holotype, female; Ochoco N. F., Oregon; Canadian Nat. Coll.). *New synonymy*

Pityophthorus depygis Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:128 (Holotype, female; Clyde, Colorado; U.S. Nat. Mus.). *New synonymy*

Pityophthorus watsoni Schedl, 1930, Canadian Ent. 62:197 (Holotype, female; Nictor Lake, New Brunswick; Canadian Nat. Coll.). *New synonymy*

Pityophthorus aurulentus Bright, 1966, Pan Pacific Ent. 42:301 (Holotype, female; Shell ridge at Walnut Creek, Contra Costa Co., California; California Acad. Sci.). *New synonymy*

The female frons of this species varies from convex to extensively flattened, with punctures moderately coarse to minute, and with or without vestiture. The vestiture, when present, may be minute to very long. Any combination of these variations may be found in pure culture in a local area or all may occur there. Following the study of the holotypes and type series of *Pityophthorus murrayanae* Blackman, *P. gracilis* Swaine, *P. cutleri* Swaine, *P. exilis* Swaine, *P. depygis* Blackman, *P. watsoni* Schedl, and *P. aurulentus* Bright, more than 2,000 other specimens, and numerous field observations, it was concluded that all represent the same species. Similar variability of the female frons occurs in *Pityophthorus cariniceps* LeConte, the *P. balsameus* complex of species, *Ips tridens* (Mannerheim), and *I. pilifrons* Swaine.

Pityophthorus ornatus Blackman

Pityophthorus ornatus Blackman, 1928, New York St. Coll. For., Syracuse, Tech. Pub. 25:102 (Holotype, female; Manitou, Colorado; U.S. Nat. Mus.)

Pityophthorus limatus Wood, 1964, Great Basin Nat. 24:65 (Holotype, female; Sanford Canyon, Dixie N. F., Utah; Wood Coll.). *New synonymy*

The female holotypes of *Pityophthorus ornatus* Blackman and *P. limatus* Wood and 111 other specimens were examined. Of the 10 series examined, 4 from Colorado and 6 from Utah, the host was *Picea pungens* for 8 of them; 2 were from *Pinus* and both appeared to be accidental associations. The population in Colorado has the vestiture on the female frons longer, particularly on the margins, and apparently less dense. The host and differences on the female frons led to the description of *limatus*. It is now recognized as a slight geographical variant and should be placed in synonymy as indicated above.

Pityophthorus pseudotsugae Swaine

Pityophthorus pseudotsugae Swaine, 1918, Dom. Canada Dept. Agric. Ent. Br. Tech. Bull. 14(2):99 (Holotype, female; BX Mountain, Vernon District, British Columbia; Canadian Nat. Coll.)

Pityophthorus thatcheri Bright, 1977, Great Basin Nat. 36:442 (Holotype, female; Big Sandy Meadow, S28, T5S, R2E, California; Wood Coll.). *New synonymy*

The female holotypes of *Pityophthorus pseudotsugae* Swaine and *P. thatcheri* Bright and more than 500 other specimens of this species were examined and compared directly to one another, including the entire type of series of *P. thatcheri* and several other specimens taken in series with it. It is apparent that the series named *P. thatcheri* was either accidental in *Pinus lambertiana* or else an error occurred in recording the host. These specimens are normal representatives of *P. pseudotsugae* and must be placed in synonymy as indicated above.

Pityophthorus pullus (Zimmermann)

Crypturgus pullus Zimmermann, 1868, Trans. Amer. Ent. Soc. 2:143 (Holotype, female; South Carolina; Mus. Comp. Zool.); Bright, 1976, Coleopt. Bull. 30:187 (?Lectotype)

Pityophthorus bisulcatus Eichhoff, 1869, Berliner Ent. Zeitschr. 12:274 (Holotype, sex?; America borealis; apparently lost with Hamburg Mus.). *New synonymy*

The type series of *Pityophthorus bisulcatus* Eichhoff apparently was lost in the destruction of the Hamburg Museum. Eichhoff (1878, Mém. Soc. Roy. Sci. Liége (2)8:185) indicated possible synonymy of his species with *P. pullus* Zimmermann. The size of *bisulcatus* was given as "¾ lin." (1.7 mm) in 1869, but 1.5 mm in 1878. If the 1.5 mm measurement is correct, it would almost certainly place *bisulcatus* in synonymy with *annectens;* if the 1.7 mm measurement is correct it might place it in synonymy with either *pullus* or *confusus* Blandford. Since the Eichhoff description does not treat anatomical areas that would distinguish *bisulcatus* from *confusus* or *annectens* (the only other species of comparable size from the southeastern United States where Eichhoff received specimens), it appears advisable to assume that Eichhoff, 1878, was correct and place his species in synonymy under *pullus*.

Scolytodes levis Blackman

Ctenophorus laevigatus Chapuis, 1869 (nec. Ferrari, 1867), Synopsis des Scolytides, p. 49 (Syntypes, males; Colombie; Brussels Mus.). *Preoccupied*

Hexacolus levis Blackman, 1943, Proc. U.S. Nat. Mus. 94(3174):382 (Holotype, female; Paraiso, Canal Zone, Panama; U.S. Nat. Mus.)

Scolytodes chapuisi Wood, 1977, Great Basin Nat. 37:210 (Replacement name). *New synonymy*

Ctenophorus laevigatus Chapuis was based on two male syntypes. These were compared to my long series from Colonia Tovar, El Laurel, and Ranch Grande, Venezuela, and apparently agree in all details. Females from my series were compared to the female holotype of *Hexacolus levis* Blackman and were found to be conspecific. Assuming that the association of males is correct, the name *levis* has priority and should be used to designate this species.

New Species

Pityophthorus crotonis, n. sp.

This large species is remotely related to *Conophthocranulus blackmani* Schedl, but is distinguished by numerous characters described below.

Male.— Length 3.8 mm (paratypes 3.2-3.9 mm), 2.5 times as long as wide; color very dark brown.

Frons convex, an indistinct, feeble, transverse impression near middle; surface smooth, shining, coarsely, closely punctured; vestiture short, inconspicuous.

Pronotum 1.03 times as long as wide; sides almost straight and parallel on basal half, rather broadly rounded in front; anterior margin armed by 10 low serrations; summit at middle; anterior half with low, dense, confused asperities; posterior half smooth, shining, impressed points fine, abundant, punctures fine, rather close. Vestiture sparse, confined to marginal areas.

Elytra 1.4 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, broadly rounded (feebly bi-emarginate) behind; striae 1 weakly impressed; surface smooth, shining, punctures moderately coarse, close, confused. Declivity very steep, rather broadly bisulcate; striae 1 very strongly, 2 strongly impressed, punctures in rows, fine, strongly impressed; interstriae 1 moderately elevated, broadly rounded, with dense impressed points and a few punctures, armed at base by a row of about four fine denticles, 2 slightly wider than 1, weakly convex, smooth, shining, with numerous impressed points, 3 elevated as high as 1, armed by a row of about 6-10 coarse denticles, lateral areas rather coarsely punctured. Vestiture apparently derived from odd-numbered interstriae, very long, absent on declivital interstriae 1.

Female.— Similar to male except apparently smaller, denticles on anterior margin of pronotum and on elytral declivity smaller, strial punctures on disc usually in distinguishable rows.

Type Locality.— Thirty km east of Merida, Merida, Venezuela.

Type Material.— The male holotype, female allotype, and 93 paratypes were taken at the type locality on 8-I-1970, 2500 m, No. 220, *Croton* boles and limbs, by me. Two paratypes are from 20 km W Merida, Merida, Venezuela, 10-X-1969, No. 45, same elevation, host, and collector.

The holotype, allotype, and paratypes are in my collection.

Scolytodes canaliculus, n. sp.

This species is distinguished from the remotely allied *levis* Blackman by the larger size and by numerous other characters described below.

Female.— Length 3.0 mm (paratypes 2.5-3.1 mm), 2.4 times as long as wide; color yellowish brown to light brown.

Frons uniformly, moderately convex; surface reticulate except smooth, shining, and impunctate on a subtriangular area extending from median third of epistomal area to an indefinite median point two-thirds of distance to upper level of eyes, reticulate area with rather numerous, fine punctures near margins of shining area; vestiture of fine, rather sparse, long hair on area below eyes. Eyes separated above by less than twice width of an eye. Antennal scape ornamented by a tuft of about 20 long setae.

Pronotum 1.0 times as long as wide; about as in *levis;* anterior slope unarmed, surface reticulate, punctures fine, rather close but distinctly larger than in *levis.*

Elytra 1.4 times as long as wide, 1.6 times as long as pronotum; sides straight on basal two-thirds, very slightly wider at base of declivity; striae not impressed except 1 moderately from base, punctures moderately coarse, rather deep; interstriae shining, almost smooth (obscurely reticulate in some areas), almost three times as wide as striae, punctures fine, close, uniseriate on 2 and 3, moderately confused on other interstriae. Declivity steep, shallowly sulcate; striae 1 strongly impressed; interstriae 1 convex, lateral areas ascending from striae 1 rather abruptly to rounded summit at striae 3; sculpture about as on disc. Vestiture of a few minute strial and interstrial setae (shorter than distance equal to diameter of a puncture), mostly on posterior half, and sparse rows of rather long interstrial setae on and near declivity.

MALE.— Similar to female except frons uniformly reticulate, shining area and most long setae absent, antennal scape without tuft of long hair.

TYPE LOCALITY.— La Carbonera Experimental Forest, about 50 km (airline) west of Merida, Merida, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 140 paratypes were taken at the type locality on 9-XII-1969, 2,500 m, No. 177, from *Clusia* branches, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes constrictus, n. sp.

This species is distinguished from *varius* Wood by the much finer pronotal and elytral punctures, by the greatly reduced female frontal pubescence, by the more nearly flattened elytral declivity, and by other characters described below.

FEMALE.— Length 2.7 mm (paratypes 2.5-2.8 mm), 2.8 times as long as wide; color almost black, some specimens with elytra uniformly dark brown.

Frons flat on lower two-thirds, moderately convex above; smooth and shining on flattened area, reticulate above, punctures fine, distinctly impressed; vestiture sparse, rather short, inconspicuous.

Pronotum 1.17 times as long as wide, sides widest one-fourth pronotum length from anterior margin, rather strongly constricted on posterior half; summit in front of middle, anterior slope finely, closely asperate; posterior areas mostly smooth, shining, some areas of weak reticulation in some specimens; punctures mostly fine, rather close, distinctly impressed. Vestiture of fine, long, moderately abundant, hairlike setae.

Elytra 1.7 times as long as wide, 1.5 times as long as pronotum; outline about as in *varius;* striae not impressed, punctures fine, spaced by twice diameter of a puncture; intestriae three times as wide as striae, smooth, shining, punctures slightly smaller and spaced equal to those of striae. Declivity rather steep, very broadly convex; sculpture similar to disc, but all punctures much smaller, striae not impressed. Vestiture as in *varius,* but slightly shorter.

MALE.— Similar to female except frons more strongly convex, with punctures finer.

TYPE LOCALITY.— Piedras Blancas, 11 km west of Medellin, Antioquia, Colombia.

TYPE MATERIAL.— The female holotype, male allotype, and 27 paratypes were taken at the type locality on 17-VII-1970, 2300 m, No. 688, from *Baccharus,* by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes contractus, n. sp.

This species is distinguished from *varius* Wood by the slightly more slender body form, by the sparse, shorter, female frontal pubescence, and by the smaller pronotal and elytral punctures. It is distinguished from *constrictus* Wood by the brownish color, by the coarser pronotal and elytral punctures, and by the more convex declivity, with the striae clearly impressed.

FEMALE.— Length 2.8 mm (paratypes 2.5-

3.1 mm), 2.7 times as long as wide; color brown, anterior half of prothorax and head usually dark brown.

Frons as in *constrictus* except lateral areas reticulate to epistoma, punctures distinctly larger.

Pronotum as in *constrictus* except punctures distinctly larger.

Elytra as in *constrictus* except striae feebly impressed, punctures larger, closer, spaced by less than diameter of a puncture, interstriae twice as wide as striae, punctures closer, declivity more strongly convex, with striae weakly impressed and punctures slightly larger. Vestiture about as in *varius*.

MALE.— Similar to female except lower frons more distinctly convex.

TYPE LOCALITY.— Thirteen km southwest of El Vigía, Merida, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 34 paratypes were taken at the type locality on 22-X-1969, 100 m, No. 95, from a large vine (liana), by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes festus, n. sp.

This species is distinguished from *atratus* Blandford by the different frons in both sexes, by the much coarser punctures on the pronotum and elytra, and by the longer elytral setae.

FEMALE.— Length 2.8 mm (paratypes 2.5-2.8 mm), 2.0 times as long as wide; color black.

Frons almost flat to feebly concave on lower half, about as in *jucundus* Wood except reticulation less distinct, punctures slightly larger, less abundant.

Pronotum about as in *atratus* except punctures much larger, deep, interspaces equal to about twice diameter of a puncture. Glabrous except near margins.

Elytra about as in *atratus* except striae not impressed, strial and interstrial punctures slightly larger, mostly in rows, declivital striae not impressed, punctures much smaller than on disc, declivital tubercles smaller. Vestiture longer than in *atratus*, half as close, each seta on disc as long as distance between rows, not longer on declivity; short recumbent strial hair present on lower and lateral areas of declivity.

MALE.— Similar to female except pronotal asperities larger, more abundant, frons very different. Frons similar to male *jucundus* except upper margin of transverse impression gradually elevated, lower margin abrupt, crest more uniformly elevated, median summit not evident.

TYPE LOCALITY.— Piedras Blancas, 11 km west of Medellin, Antioquia, Colombia.

TYPE MATERIAL.— The female holotype, male allotype, and nine paratypes were taken on 17-VII-1970, 2,300 m, No. 691, from petioles of fallen *Cecropia* leaves.

The holotype, allotype, and paratypes are in my collection.

Scolytodes jucundus, n. sp.

This species is distinguished from *atratus* Blandford by the larger size and by the different frons in both sexes and declivity as described below.

FEMALE.— Length 3.3 mm (paratypes 3.0-3.5 mm), 2.1 times as long as wide; color very dark brown to almost black.

Frons about as in *atratus* except surface between punctures reticulate, median callus entirely absent on lower half.

Pronotum 1.1 times as long as wide; about as in *atratus* except reticulation slightly more strongly impressed, punctures slightly more numerous.

Elytra 1.3 times as long as wide, 1.5 times as long as pronotum; about as in *atratus* except striae less distinctly impressed, all punctures slightly smaller, granules on declivity slightly smaller, setae more widely spaced, apparently shorter.

MALE.— Similar to female except frons above level of antennal insertion convex, reticulate, rather finely punctured; area at level of antennal insertion broadly, rather strongly, transversely impressed, lower margin of impression forming a transverse crest above flattened epistomal area, crest with a median and a pair of lateral low summits; pronotal asperities larger and more numerous than in female.

Type Locality.— Ranch Grande, Aragua, Venezuela.

Type Material.— The female holotype, male allotype, and 17 paratypes were taken at the type locality on 9-IV-1970, 1,100 m, No. 403, from petioles of fallen *Cecropia* leaves, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes opacus, n. sp.

This species is distinguished from *opimus* Wood by the smaller size, by the darker color, and by other characters described below.

Female.— Length 3.0 mm (paratypes 2.5-3.0 mm), 2.0 times as long as wide; color very dark brown.

As in *opimus* except frons more distinctly convex, granules on elytral disc slightly larger, punctures on sides of elytra slightly larger, deeper, elytral vestiture slightly stouter, shorter.

Type Locality.— Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 93 paratypes were taken at the type locality between Teleferico Stations 2 and 3 on 27-II-1970, near 3,000 m, No. 331, from the 10 cm bole of a tree with extremely large, simple leaves, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes opimus, n. sp.

This species represents the extreme expression of characters in a group of species allied to *punctatus* Eggers. Superficially it resembles *Gymnochilus*, but fundamental characters clearly place it in *Scolytodes*. It is distinguished by the large size, by the stout form, and by the contour and sculpture of the elytra. Some of Eggers' "*Problechilus*" species are closely related.

Female.— Length 3.3 mm (paratypes 2.7-3.5 mm), 1.9 times as long as wide; color brown.

Frons almost flat below level of antennal insertion, an indistinct, transverse impression above this point, weakly convex above; a low, oblique carina from margin of antennal insertion to lateral part of epistomal margin; surface strongly reticulate, punctures very fine, moderately close, those above level of antennal insertion finely granulate; vestiture of short, fine, moderately abundant, inconspicuous hair.

Pronotum 1.0 times as long as wide, subcircular in outline; evenly, rather strongly arched from anterior margin to base; anterior margin armed by a row of about a dozen fine serrations; surface reticulate; anterior area armed by numerous small, isolated asperities, these decrease in size but not in density, disappear on basal fifth, and are replaced by fine, close, moderately deep punctures. Vestiture fine, short, inconspicuous, covering entire surface.

Elytra 1.15 times as long as wide, 1.4 times as long as pronotum; sides weakly arcuate and subparallel on basal two-thirds, broadly rounded behind; declivity commencing on basal third near suture, near middle in lateral areas; striae not impressed, punctures very minute, distinct; interstriae smooth, shining, about 6 to 10 times as wide as striae, punctures similar to those of striae, confused, those near declivity granulate (subvulcanate). Declivity gradual on upper half, steep below, convex except shallowly sulcate toward striae 1; striae 1 moderately, rather broadly impressed, ascending gradually to striae 3; sculpture as on disc, most punctures on interstriae 1 and 2 weakly, irregularly subvulcanate. Vestiture of moderately abundant hair, setae on declivity short, longer on disc, with many interstrial setae on disc exceedingly long (these long setae abraded on older specimens.

Male.— Similar to female in all respects.

Type Locality.— La Carbonera Experimental Forest, about 50 km (airline) west of Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 27 paratypes were taken at the type locality on 9-XII-1969, 2,500 m, No. 172, from an unidentifiable vine (liana) 5-8 cm in diameter, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes praeceps, n. sp.

This species is distinguished from *canaliculus* Wood by the very different frons and elytra as described below.

Female.— Length 2.8 mm (paratypes 2.4-2.8 mm), 2.4 times as long as wide; color dark brown.

Frons weakly convex, median half from epistoma to three-fourths distance to upper level of eyes smooth, shining, impunctate, lateral and upper areas finely, rather closely punctured; vestiture of moderately abundant, very long hair on punctured areas. Eyes rather widely separated above. Antennal scape with about a dozen long setae.

Pronotum about as in *canaliculus* except punctures larger, closer, interspaces slightly wider than diameter of a puncture.

Elytral outline about as in *canaliculus;* striae not impressed, punctures rather small, deep; interstriae smooth, shining, three times as wide as striae, punctures mostly uniseriate, a few of those on 1 and 2 near declivity finely granulate. Declivity very steep, broadly convex; striae 1 moderately, 2 and 3 weakly impressed; sculpture about as on disc except interstriae 1-3 each with a row of fine granules on upper two-thirds. Vestiture of minute strial hair and rows of stout, erect, rather closely spaced bristles; each bristle on disc about as long as distance between rows, on declivity about two-thirds this length.

Male.— Similar to female except frons more strongly convex, uniformly reticulate, vestiture sparse, inconspicuous.

Type Locality.— Piedras Blancas, 10 km east of Medellin, Antioquia, Colombia.

Type Material.— The female holotype, male allotype, and 11 paratypes were taken at the type locality on 15-VII-1970, 2,500 m, No. 660, from a *Clusia* branch, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes serenus, n. sp.

This species is distinguished from *levis* (Blackman) by the much larger size, by the weak pronotal asperities, and by the larger pronotal and elytral punctures.

Female.— Length 2.8 mm (paratypes 2.6-3.0 mm), 2.5 times as long as wide; color pale brown, elytra usually yellowish brown.

Frons as in *levis* except more strongly flattened to vertex (not receding).

Pronotum similar to *levis* except anterior third very finely asperate (asperities visible only when light comes from appropriate angle); reticulation on posterior areas coarser, punctures slightly larger. Glabrous.

Elytra similar to *levis* except strial and interstrial punctures larger and deeper; interstriae about four times as wide as striae, punctures spaced by one to two diameters of a puncture, about as large as those of striae, in almost definite rows; sculpture on declivity about as on disc except all punctures slightly smaller.

Male.— Similar to female except frons weakly convex on upper two-thirds, subglabrous, pronotal asperities distinctly larger.

Type Locality.— La Mucuy, 20 km west of Merida, Merida, Venezuela.

Type Material.— The female holotype, male allotype, and 37 paratypes were taken at the type locality on 10-X-1969, 2,500 m, No. 46, from a Martiño branch (presumably *Meriana* sp.), by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes suturalis, n. sp.

This species is distinguished from *atratus* (Blandford) by the slightly smaller size, by the different frons in both sexes, by the slightly larger pronotal punctures, and by the very different elytra.

Male.— Length 2.7 mm (paratypes 2.5-2.7 mm), 2.1 times as long as wide; color very dark brown.

Frons about as in *jucundus* Wood except punctures fine, transverse impression larger, much deeper, transverse crest much higher, subacute, almost uniformly elevated; upper areas reticulate, rather coarsely punctured; vestiture inconspicuous.

Pronotum about as in *atratus* except punctures slightly larger, interspaces averaging three to four diameters of a puncture.

Elytra resembling *atratus*. Striae 1 strongly impressed on posterior three-fourths, others narrowly, weakly impressed, punctures very fine, subconfluent, rows not straight; interstriae about five times as wide as striae, smooth, shining, punctures mostly replaced by rounded granules almost to base, uniseriate. Declivity slightly steeper than in *atratus*, striae narrowly, rather deeply impressed, punctures as large as on disc but not as close, interstriae more narrowly convex, granules slightly closer, more regular, vestiture much stouter, slightly longer, extending to base.

FEMALE.— Similar to male except lower frons about as in *jucundus* except more distinctly concave, reticulation absent; strial impressions not as strong as in male and granules smaller, particularly on disc.

TYPE LOCALITY.— El Laurel Experimental Farm, 12 km southwest of Caracas, Venezuela.

TYPE MATERIAL.— The male holotype, female allotype, and five paratypes were taken at the type locality on 1-V-1970, 1,300 m, No. 461, from petioles of fallen *Cecropia* leaves, by me.

The holotype, allotype, and paratypes are in my collection.

Scolytodes varius, n. sp.

This species apparently is allied to *punctatus* Eggers, but it is distinguished by the slender body form, by the narrower posterior third of the pronotum, and by numerous other characters described below.

FEMALE.— Length 2.7 mm (paratypes 2.5-3.1 mm), 2.5 times as long as wide; color very dark brown except yellowish brown on intestriae 2-4 to 2-6 and declivity; males yellowish brown except anterior third of pronotum darker.

Frons broadly flattened to feebly concave from epistoma to upper level of eyes; surface smooth, shining, rather coarsely, closely, almost uniformly punctured except a median, impunctate callus on median fourth at level of antennal insertion; vestiture moderately abundant, fine, very long.

Pronotum 1.12 times as long as wide; widest on anterior half, sides weakly constricted, anterior margin semicircularly rounded, unarmed; anterior slope finely, closely asperate; posterior areas coarsely, rather closely punctured, surface obscurely, irregularly subreticulate. Vestiture fine, very long, rather abundant.

Elytra 1.5 times as long as wide, 1.4 times as long as pronotum; sides almost straight and parallel on basal two-thirds, rather broadly rounded behind; striae not impressed, punctures moderately coarse, deep, spaced by diameter of a puncture; interstriae shining, almost smooth, punctures uniseriate, as close as and almost as large as those of striae. Declivity steep, broadly convex; sculpture as on declivity except punctures very slightly smaller. Vestiture of fine, long strial and interstrial hair, some interstrial setae three or more times as long as distance between rows.

MALE.— Similar to female except color uniformly pale over most of body, frons distinctly convex on upper half, its vestiture sparse, inconspicuous.

TYPE LOCALITY.— La Mucuy, 20 km west of Merida, Merida, Venezuela.

TYPE MATERIAL.— The female holotype, male allotype, and 116 paratypes were taken at the type locality on 12-XI-1969, 2,500 m, No. 129, from a tree branch, by me.

The holotype, allotype, and paratypes are in my collection.

NECTAR-SUGAR CONCENTRATIONS AND FLOWER VISITORS IN THE WESTERN GREAT BASIN

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Abstract.— Nectar-sugar concentrations and major flower visitors were determined for 15 species of plants in the Eagle Lake area of Northeastern California. Sugar concentrations for 12 of these are reported for the first time, with means ranging from a low of 10 percent in *Mentzelia laevicaulis* to a high of 63 percent in *Ranunculus uncinatus*. The utilization of the various nectar concentrations varied with the type of flower visitor as well as with the habitat and distributional ranges of the plant and/or animal. Hummingbirds and hawkmoths were not observed visiting the flowers they typically visit in other areas (e.g. *Aquilegia* and *Ipomopsis*, or *Oenothera*), but here preferred more concentrated nectar (*Cirsium* spp., with $\bar{x}$ of 57 percent sugar). Specialization in nectar use is reported at the generic and specific level in Hymenoptera and Lepidoptera; solitary bees, as a whole, used slightly less concentrated nectar ($\bar{x}$ = 38 percent sugar) than butterflies ($\bar{x}$ = 44 percent sugar).

Numerous studies dealing with plant-animal interactions report the importance of flower characteristics such as shape, color, and odor in determining which animals visit a particular species. Recent studies have shown that a correlation also exists between the type of animals which visit a plant and its nectar composition, including the volume of nectar (Heinrich and Raven 1972), types of sugars (Percival 1961, 1965, Wykes 1952), concentration of sugars (Watt, Hoch, and Mills 1974, Baker 1975), and other nectar constituents such as amino acids and proteins (Baker and Baker 1975). In this paper we present data on nectar-sugar concentrations in several nectars utilized by different classes of flower visitors in our study area at the south end of Eagle Lake, Lassen County, northeastern California. The area is characterized by open forests of western juniper (*Juniperus occidentalis*) and Jeffrey pine (*Pinus jeffreyi*), and by more open areas dominated by big sagebrush (*Artemisia tridentata*) and rabbitbrush (*Chrysothamnus nauseosus*). The plant populations used in this study (June to August 1976) were located at elevations between 1530 and 1800 m above sea level; plant names are according to Munz and Keck (1968).

Methods and Materials

Nectar was collected in the field with 10 μl microcapillary pipettes (Drummond Scientific Co.). For extraction from narrow, tubular flowers, the pipettes were drawn out into fine points. Approximately 24 hours prior to nectar extraction the flowers were covered with sheets of porous lens tissue (15 x 20 cm) to keep flower visitors from removing the nectar. The percentage of sugar was determined in the field with a Bellingham and Stanley pocket refractometer, which read up to 50 percent. For nectars more concentrated than this, and for samples smaller than 3–4 μl, an equal amount of distilled water was measured in a second calibrated pipette, and mixed with the nectar sample on the stage of the refractometer. The reading obtained is based on the refractive index of the solution. Nectar sugars in flowering plants consist mainly of sucrose, fructose, and glucose in varying proportions; sucrose is the most widespread and usually predominates (Percival 1961). Sucrose, fructose, and glucose give similar refractive index readings for equal percent solutions by weight (Wykes 1952); therefore, we report our readings as "nectar-sugar," "sucrose," or simply "sugar."

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Flower visitor data were obtained through observations and collection rather than by consulting the literature. On several occasions flower visitors were observed and collected during three time periods (morning, afternoon, and evening), with approximately equal time being spent at each plant species. Flower visitors referred to below as "major" are those which were observed on the flowers on each day (although not necessarily during all three time periods). Representative insect specimens are on file in the Entomology Museum, California State University, Chico.

Results and Discussion

The nectar-sugar concentrations of the 15 species sampled are presented in Table 1. Means of our readings agree fairly closely with those previously reported for three species: *Aquilegia formosa*, 25 percent (vs 32 percent by Baker 1975); *Ipomopsis aggregata*, 25 percent (vs 22 percent by Watt, Hoch, and Mills 1974, and ca 23 percent by Hainsworth 1973); *Oenothera hookeri*, 32 percent (vs 26 percent by Stockhouse 1975). The mean percent sugar contained in the nectars ranged from a low of 10 percent in *Mentzelia laevicaulis* to a high of 63 percent in *Ranunculus uncinatus*. A large variation in nectar-sugar concentrations was also observed within most species. *Asclepias fascicularis*, the most extensively studied species, had nectar-sugar readings ranging from 16 to 72 percent. The openly exposed nectar of this species makes it highly susceptible to environmental factors which cause evaporation and/or dilution; these factors can account, in part, for the wide range of nectar concentrations observed (Stopher, Schlising, and Gut, ms in preparation).

Table 2 is a summary of the major flower visitor types found on flowers of the 15 species of plants studied. Wasp, fly, beetle, and ant visitor types are listed here (and wasps and ants again in Table 3), but since there are no detailed data available for these types they will not be further discussed in

Table 1. Fifteen plant species studied near Eagle Lake, June to August 1976, arranged according to nectar-sugar concentrations. Major flower visitors observed are also listed for each species, roughly in order of importance. Visitor code letters refer to the abbreviations listed in Tables 2–4. Plant names are from Munz and Keck (1968).

Species	Percent Sugar Mean	Percent Sugar Range	No. Flowers Sampled	Flower Visitors
Ranunculus uncinatus	63	62-63	3	Sb Wp Bf Dl Ad Vp Ly Sy Fl Bt At
Cirsium californicum	59	44-74	20	Sb Bb Wp Bf Hm Xy An Os Ag Vp Sp Pp Sy Ml Lm Fl Bt At
Cirsium breweri	54	35-66	28	Sb Bb Hk Hm An Mg Dl Sp
Agastache parvifolia	50	41-76	14	Sb Bf An Os Dl Sy Bt
Asclepias fascicularis	47	16-72	365	Sb Ap Bb Wp Bf Xy An Mg Dl Sh Hy Vp Sp Dn Pp Ly Lm Fl Bt
Scrophularia californica	43	39-49	5	Sb Wp Dl Hy Vp Fl At
Asclepias speciosa	33	21-42	66	Sb Ap Wp Bf Cr An Cl Mg Dl Hy Vp Sp Sn Pp Ly Fl Bt
Oenothera hookeri	32	23-38	25	
Monardella odoratissima	31	17-44	12	Sb Bf Os Sy Ml Bt
Ipomopsis aggregata	25	17-36	33	Fl
Aquilegia formosa	25	14-40	94	Sb Cr
Schoenolirion album	22	16-33	14	Sb Ap Bb Wp Bf Cr Cl Hy Vp Ph Bt At
Pentstemon speciosus	21	14-28	8	Sb Cr Os Dl Hy At
Nocotiana attenuata	21	14-33	27	
Mentzelia laevicaulis	10	7-18	27	Sb Ap Dl Fl
Overall	36	7-76	741	

this paper. All bees other than the honeybee and bumblebees have been grouped under solitary bees. Solitary bees comprise the largest number of flower visiting species in the area and were found on all but three of the plant species studied.

With the exception of *Asclepias fascicularis* (mean nectar concentration of 47 percent sugar), honeybee visits were restricted to the flowers with the more dilute nectars (i.e., concentrations below 35 percent). All of the other flower visitor types preferred more concentrated nectars. However, all of these visitor types had representative species which were found on flowers containing a dilute nectar. *Schoenolirion album*, with an average nectar-sugar concentration of 22 percent, was an especially utilized dilute nectar source. Possible reasons for this were easy accessibility to the nectar, many flowers per raceme, and the fact that this species was one of the very few species locally in flower at the time. Two average sugar concentrations are given for both hawkmoth and hummingbird visitor types due to discrepancies between the flowers they typically visit and the flowers they visited in the study area (see below).

TABLE 2. Major flower-visitor types and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitor Type	No. Species of Flowers Visited	Percent Sugar	
		Mean	Range
Solitary bee (Sb)	12[a]	38	10-63
Honeybee (Ap)	4	28	10-47
Bumblebee (Bb)	4	46	22-59
Wasp (Wp)	6	45	22-63
Butterfly (Bf)	7	44	22-63
Hawkmoth (Hk)	1	54	
(Hawkmoth	2[b]	27	21-32)
Hummingbird (Hm)	2	57	54-59
(Hummingbird	2[c]	25	25-25)
Fly (Fl)	7	38	10-63
Beetle (Bt)	7	40	22-63
Ant (At)	6	38	25-59
Overall	15	36	10-63

[a] Abbreviations by visitor type names are listed in Table 1 to show which species of flowers were visited.

[b] No visitors were observed, but these plants are expected to be hawkmoth visited (see text).

[c] No visitors were observed, but these plants are expected to be hummingbird visited (see text).

HUMMINGBIRDS.— There was a large difference in the concentration of sugars found in the nectar of the four "hummingbird flowers" but these plants can be grouped into two pairs with similar concentrations (Table 2). One pair consists of two "typical" hummingbird flowers (e.g., Grant and Grant 1968), *Ipomopsis aggregata* and *Aquilegia formosa*, both of which had mean sugar concentrations of 25 percent here, but were not visited by birds. The other two species, *Cirsium californicum* and *C. breweri*, had 59 percent and 54 percent sugar, respectively; these were heavily visited by hummingbirds

TABLE 3. Major families and genera of Hymenoptera and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitors	No. Species of Flowers Visited	Percent Sugar	
		Mean	Range
Anthophoridae	8	39	21-59
Xylocopa (Xy)	2[a]	53	47-59
Ceratina (Cr)	4	25	21-33
Anthophora (An)	5	49	33-59
Apidae	6	38	10-59
Apis (Ap)	4	28	10-47
Bombus (Bb)	4	46	22-59
Megachilidae	8	40	21-59
Osmia (Os)	4	40	21-59
Chelostomoides (Cl)	2	28	22-33
Megachile (Mg)	3	45	33-54
Halictidae	9	42	10-63
Dialictus (Dl)	8	40	10-63
Agapostemon (Ag)	1	59	
Sphecodes (Sh)	1	47	
Colletidae	5	33	21-47
Hylaeus (Hy)	5	33	21-47
Andrenidae	1	63	
Andrena (Ad)	1	63	
Formicidae (At)	6	38	21-59
Vespidae (Vp)	6	44	22-63
Sphecidae (Sp)	4	48	33-59
Overall	12	38	10-63

[a] Abbreviations by bee genus and by nonbee family names are listed in Table 1 to show which species of flowers were visited.

in the study area. Moldenke (1976) does list hummingbirds as especially important pollinators for the genus *Cirsium*. Exact identifications could not be made, but anna's, calliope, and rufous hummingbirds are all known to occur in the area (R. Lederer, personal communication 1977).

Since hummingbirds are high-energy demanding animals, it is advantageous for a cross-pollination-dependent plant to produce a less concentrated nectar and "force" the potential pollinator to visit the maximum number of flowers in order to fulfill its own energy needs (Baker 1975, Heinrich and Raven 1972). Previous studies have found that hummingbirds prefer the less concentrated nectars (Baker 1975, Hainsworth 1973, Hainsworth and Wolf 1972). This is contradictory to our findings, in which hummingbirds did not utilize "their typical flowers" with less concentrated nectars but preferred richer food sources. This has also been found by Stiles (1976), who showed that experimental anna's hummingbirds preferred sucrose and glucose in the highest concentrations available, up to 60 percent. Factors which favor the use of nectar with a weak sugar content may include the disadvantage of a viscous nectar to a bird which must hover while feeding (Weymouth, Lasiewski, and Berger 1964), the difficulty of imbibing and swallowing a more viscous nectar (Hainsworth 1973, Weymouth et al 1964), and the need the birds have for a free water source (Baker 1975). Then what factors, other than nectar concentration, were important in determining hummingbird flower selectivity reported here? Three important factors may be plant population size and density, growth habit of the plants, and the concentrations of the different sugars in the nectar.

Investigations on the energetics of foraging by tropical hummingbirds have shown that large numbers of flower visits are required each day (Wolf, Hainsworth, and Stiles 1972). Gass, Angehr, and Centa (1976) reported that temperate zone hummingbirds defend a territory containing 239 floral units of resource value which is equivalent to that produced by 239 *Aquilegia formosa* flowers. The population of *A. formosa* in the present study contained no more than 100 flowers on any one day. Since no hummingbirds were seen visiting *Aquilegia* here, but were common in the area, it seems density of plants may help determine nectar source. Gass et al (1976) noted that rufous hummingbirds regulate the size of their feeding territories in order to maintain food supplies at a level approximating their metabolic requirements. Also, migratory species feed in a wide variety of habitats each year under a wide range of physiological stresses. Thus, when a territory supplies insufficient energy, the birds' strategy is to seek food elsewhere. This may be the case with hummingbirds we saw, where the populations of *Cirsium breweri* and *C. californicum* were both much larger than that of *Aquilegia formosa* and were in fact the only plants seen visited by the birds.

Gass et al (1976), however, also noted that hummingbirds will feed on the nectar of a preferred species first, even if the population size is too small to meet the birds' energy requirements, and then turn to an alternate source. The fact that we did not observe any foraging on *Aquilegia* may be partially explained by noting that the plants of *Aquilegia* were growing closely interspersed with shrubs, while plants of *C. breweri* especially were located in the open only about 10 m from the *Aquilegia*. The flowers of *Aquilegia* may not have been as readily accessible and energetically favorable for nectar foraging.

The single population of *Ipomopsis aggregata* studied was also small (about 50 flowers at any time), and had the same nectar-sugar concentration as *Aquilegia* and perhaps even a similar floral unit of resource value. This may again suggest that population density could be an important factor in determining the nectar utilization strategy seen in this study.

Yet another possible factor contributing to the nectar selection of the hummingbirds is the proportions of the different sugars in the nectars. The kinds of sugars present were not determined for our Eagle Lake plants; but *Cirsium californicum* sampled elsewhere was found to have a rather high percent of glucose (58 percent) in the sugars present (I. Baker, personal communication, 1976). Stiles (1976) reported the following hierarchy of sugar preferences in several species of hummingbirds: sucrose over glucose over fructose, with an equal-parts mixture of the three falling somewhere in the middle of the preference order. A nectar containing a large percentage of glucose may be less viscous than one containing a large percentage of sucrose. Thus the high percentage of total sugars in the nectar of *C. californicum* (a potentially highly viscous nectar) may be compensated for by the high percentage of glucose; this may make the nectar less viscous, which, as noted earlier, is advantageous to the feeding of the birds.

HAWKMOTHS.— A situation similar to that with the hummingbirds existed for the hawkmoths and the flowers they visited in our study area (Table 2). No hawkmoths were collected, but common species in the area include *Sphinx perelegans* (Hy. Edw.) and *Hyles lineata* (Fabr.) (from collections at California State University, Chico, and Eagle Lake Field Station). Of the three species of potential hawkmoth flowers present, *Nicotiana attenuata* (Wells 1959) and *Oenothera hookeri* (Baker 1961, Stockhouse 1975) are "typical" hawkmoth-visited flowers (see also Moldenke 1976). They both had rather low average nectar concentrations of 21 percent and 32 percent, respectively. Baker (1975) also found hawkmoth flowers to have lower nectar concentrations similar to those of hummingbird flowers. At Eagle Lake, as with the hummingbird flowers, the hawkmoths were not seen visiting "their typical flowers." Instead, the moths preferred the flowers of *Cirsium breweri*, with a concentrated nectar ($\bar{x} = 54$ percent). Hawkmoths are homeothermic, hence high energy-demanding ing insects, and in this relatively cool region may require a more concentrated energy source. Also, plant population size was possibly a limiting factor. The two typical hawkmoth plants were represented by very small populations of about 10 individuals each, with 25 open flowers per evening; *Cirsium breweri* heads were very abundant. (Stockhouse [1975] however, found that a single flower of *Oenothera caespitosa* produces an average of 42.1 calories per flower [35 microliters of nectar per night of which approximately 32.5 percent is sugar], which he believes is a large enough potential energy source for hawkmoths even in a small population, with only 20-50 flowers open on a given night. Thus our few flowers of *O. hookeri* could also be a serviceable food source.)

HYMENOPTERANS.— A summary of the major flower-visiting Hymenoptera and the concentrations of nectars they feed on is given in Table 3. Considering the first four families listed (all bees), it is seen that at the family level the mean sugar concentration utilized varied little—from only 38 percent to 42 percent. More specific trends toward nectar selectivity can perhaps be seen within these families. The Anthrophoridae and Megachilidae each had two genera which preferred a more concentrated nectar and a third genus which preferred a more dilute nectar. Although not entirely consistent throughout the data, the genera containing the smaller-bodied species seemed to feed on the less concentrated nectars, and the larger-bodied seemed to utilize the more concentrated nectars. However, at the family level these four means do reflect bee usage, overall, of fairly concentrated nectars. Baker (1975) found the mean percentage of nectar-sugar for 60 species of California native bee flowers to be only 31 percent. In this study bees of a fifth family (Colletidae) preferred nectar with 33 percent sugars, while bees in a sixth family (Andrenidae) fed exclusively on the richer nectar (63 percent sugars) of a single plant species.

The Family Andrenidae in this study was represented by two species, *Andrena* (*Diandrena*) *cuneilabris* Viereck and *A.* (*Euandrena*) *caerulea* Smith (formerly *A. complexa*). These bees restricted their foraging to the flowers of *Ranunculus uncinatus*, which produced the most concentrated nectar (63 percent) found in our samples. In a study done in the Coast Ranges of California, *A. complexa* was found to feed exclusively in the flowers of *Ranunculus californicus* (Linsley and MacSwain 1959). Other species of *Andrena* have also been found to feed almost exclusively on various species of *Ranunculus* (Thorpe 1969, Linsley and MacSwain 1959). Host-specific relationships such as these have usually been described in terms of habitat, flower morphology, and /or pollen source specificity. If nectar concentration and sugar content values are "conservative characters," at least at the genus level (Percival 1961), then the high nectar-sugar concentration in *R. uncinatus* and perhaps other species of *Ranunculus* may also be a factor influencing these host-specific plant-insect interactions.

BUTTERFLIES.— Data for the four major families of butterflies found in this study are given in Table 4. The range of means for the nectar is only from 40 percent to 48 percent. In general, butterflies were feeding on a concentrated nectar source. Although data are not given, Baker (1975) reported that nectars of butterfly flowers are slightly less concentrated than those of bee flowers. Our study suggests the reverse: flowers visited by bees had a less concentrated nectar ($\bar{x}$ = 38 percent) than that of flowers visited by butterflies ($\bar{x}$ = 44 percent).

TABLE 4. Major families and genera of Lepidoptera and the nectar-sugar concentrations utilized (of the 15 plant species studied) near Eagle Lake, Lassen County, California.

Visitors	No. Species of Flowers Visited	Percent Sugar	
		Mean	Range
Danaidae (Dn)	2[a]	40	33-47
Papilionidae (Pp)	3	46	33-59
Lycaenidae (Ly)	3	48	33-63
Nymphalidae	6	45	22-63
Speyeria (Sy)	4	51	31-63
Melitaea (Ml)	2	45	31-59
Limenitis (Lm)	2	53	47-59
Phycoides (Ph)	1	22	
Overall	7	44	22-63

[a] Abbreviations by visitor names are listed in Table 1 to show which species of flowers were visited.

In their study on plant resources and adult butterflies in a subalpine environment, Sharp, Parks, and Ehrlich (1974) found that butterfly foraging seemed to show opportunistic use of what was available through the season, and no species-specific nectar source relationships were found. Baker and Baker (1975) reported that nectars of butterfly-pollinated flowers are high in amino acids and suggested this may be a factor involved in butterfly foraging strategies, because in most cases this is their only source of these essential chemicals as adults. In this study we did find an apparent specific relationship between a butterfly and its local nectar source. The genus *Phycoides* was represented here by a single species, *P. mylitta mylitta* (Edw.), which restricted its feeding to the flowers of a single species, *Schoenolirion album*. During this study adults were only seen foraging while this plant was in flower, although they are known to visit other flower species (personal observations; Benseler 1975). The nectar produced by this species was much more dilute ($\bar{x}$ = 22 percent) than the nectar of any of the other butterfly-visited flowers. Elsewwhere, *Colias* butterflies have been found to prefer more dilute nectars, probably due to their severe problems of water loss associated with small size (Watt, Hoch, and Mills 1974). Individuals of *Phycoides mylitta mylitta* are also small and may have severe water loss problems in the Eagle Lake area where midday readings of 35 percent relative humidity were of common occurrence. The less concentrated but abundant nectar of *Schoenolirion* may also be an evolutionary trend to early seasonal appearance of both the plant and its visitors. The lack of other flowers "competing" for this potential pollinator may also allow early-flowering *Schoenolirion album* to somewhat limit its nectar-sugar production without lowering chances for cross pollination here.

CONCLUSIONS

This study emphasizes several points with data collected in 1976. Data on just 15 species sampled show there was a wide range of nectar-sugar concentrations available to flower visitors found in the Eagle Lake area. The concentrations produced not only varied from species to species, but they also varied considerably within flowers of the same species. Some of this variation was doubtless caused by local and immediate environmental conditions, but it was still representative of the range of nectar-sugars available to flower visitors there. Various nectar-sugar concentrations were utilized by different types of flower visitors. Data on Hymenoptera and Lepidoptera visitors at the family level show some preferences in the concentrations utilized, but more pronounced preferences were found at the genus or species level of visitor. Species-specific, plant-insect interactions were seen in both of these visitor types in the Eagle Lake area, and the concentration of nectar sugars may be one of several factors influencing these relationships. Factors such as plant population size and density, flower accessibility, and the degree of physiological stress may vary from location to location and affect the utilization of nectar sources by foragers in a given area. This seemed especially true for the hawkmoth and hummingbird flowers, which were not being visited by these animals at Eagle Lake, who preferred more abundant, more concentrated, or more readily accessible nectar.

Acknowledgments

We would like to thank Robbin Thorp for identifying the bees, and Irene Baker and Roger Lederer for supplying unpublished information. We would also like to thank Tim Spira for his critical reading of the manuscript and Mark Stopher for his field assistance. We are grateful for the support of a National Science Foundation Undergraduate Research Participation Grant (SMI 76-03206) that was administered through the Eagle Lake Field Station.

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NEW GRASS DISTRIBUTION RECORDS FOR NEW MEXICO AND THE UNITED STATES[1]

Stephan L. Hatch[2]

Abstract.— New distribution records are given for 13 grasses now found in New Mexico. One of these, *Urochloa panicoides* Beauv., is a new distribution record for the United States.

Recent collections have revealed the occurrence of 13 taxa new to New Mexico and one taxon new to the United States. These occurrences are extensions to the known distributions of these species as recorded by Hitchcock (1951) and Gould (1951, 1975a, 1975b). A recent checklist for New Mexico by Martin and Castetter (1970) was used for grass distribution records for the State of New Mexico. Voucher specimens for these new records have been deposited in the New Mexico State University Herbarium (NMC).

Brachiaria ciliatissima (Buckl.) Chase

Eddy Co.: Thirty-two km east of Carlsbad, Sandia Radioactive Waste Storage Project, 18 September 1976, *Wilson sn.* (NMC). This collection is a new record for New Mexico. The species has been reported on sandy soils in Arkansas, Oklahoma, and Texas (Gould 1975b).

Bromus diandrus Roth

Catron Co.: Eight km west of Glenwood, elevation 2621 m, 17 October 1976, *Stockman sn.* (NMC). This is a new record for New Mexico. Previously reported from Arizona (Gould 1956) and Texas (Gould 1975b).

Grant Co.: Locally abundant 25 km west of Silver City, 25 April 1977, *Bodenchuk 20* (NMC).

Bromus mollis L.

Dona Ana Co.: Infrequent 1 km south of the junction of University Ave. and Interstate 25, elevation 1189 m, 4 March 1977, *Kolo 7* (NMC). Growing between the frontage road and the golf course in Las Cruces. This is a new record for New Mexico. Previously reported from Arizona (Gould 1956) and Texas (Gould 1975b).

Bromus rubens L.

Dona Ana Co.: Locally abundant on roadsides at the junction of Interstate 25 and highway 70 N.E. of Las Cruces, 10 April 1977, *Hatch 2399* (NMC). This collection is a new distribution record for New Mexico. This introduced species has been reported from the adjacent states of Arizona (Gould, 1951) and Texas (Gould 1975a).

Otero Co.: Locally abundant on disturbed sites, 1 km south of the White Sands Missile Range, 5 March 1976, *Williams sn.* (NMC).

Eremopyron triticeum (Gaertn.) Nevski

San Juan Co.: Locally abundant as a roadside weed, 4.7 km east of Shiprock along highway 55, 12 August 1976, *Hatch 2242* (NMC). This collection is a new record for New Mexico. This introduced species from southern Russia has been reported in Montana, Idaho, and Washington (Hitchcock 1951) and collected in Utah's Box Elder County and Emery County.

Muhlenbergia villosa Swallen

Otero Co.: Rare in a small patch, east of Orogrande on Otero Mesa, 24 September 1976, *Spellenberg 4565* (NMC). This collection is a new record for New Mexico. The taxon was previously reported as endemic to Texas (Gould 1975b).

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Panicum texanum Buckl.

Dona Ana Co.: Locally abundant as a weed on ditchbanks and in cultivated fields, 3.5 km south of Las Cruces along highway 142, 9 October 1976, *Placker sn.* (NMC). This is a new record for New Mexico. Previous reports of collections have been made in Arizona (Gould 1951) and Texas (Gould 1975a). The species is adapted to disturbed conditions of cultivated land and was probably introduced with crop seed from other states.

Schismus arabicus Nees

Dona Ana Co.: Abundant locally as an adventive grass on the New Mexico State University campus at Las Cruces, 5 March 1976, *Williams sn.* (NMC). This is a new record for New Mexico. This introduced grass has been reported from Arizona, California (Gould 1951), and Nevada (Hitchcock 1951). Hitchcock (1951) reported the grass to be a good winter forage grass that was "apparently" spreading rapidly.

Setaria adhaerans (Forsk.) Chiov.

Dona Ana Co.: Locally abundant as an adventive on disturbed sites throughout New Mexico State University campus and Las Cruces, 29 September 1976, *Hatch 2321* (NMC). Reported from the Trans-Pecos region of Texas, Bermuda, Cuba, Mexico, and Central America (Gould 1975b). This record is new for New Mexico and is the second state having a distribution record in the United States.

Setaria ramiseta (Scribn.) Pilger

Chavez Co.: An abundant, native perennial grass, growing 40 km east of Hagerman along highway 31 on the caprock, 10 August 1976, *Ellsworth 16* (NMC). New record for New Mexico. Previously reported from Texas and northeastern Mexico (Gould 1975b).

Triplasis purpurea (Walt.) Chapm.

Eddy Co.: Thirty-two km east of Carlsbad, Sandia Radioactive Waste Storage Project on sandy soils, 18 September 1976, *Wilson sn.* (NMC). Reported from west Texas and Oklahoma (Gould 1975b). This taxon is new to New Mexico.

Urochloa panicoides Beauv.

Dona Ana Co.: Occasional weed in lawns at New Mexico State University, Las Cruces, 26 August 1976, *Spellenberg 4480* (NMC). This is a new distribution record for New Mexico and the United States. the species occurs in Africa and South America. The specimen was identified by Jose F. M. Valles from Texas A & M University, College Station, Texas.

Vulpia myuros (L.) K. C. Grelin

Dona Ana Co.: Frequent between "A" Mountain and Interstate 25 southeast of Las Cruces, 10 April 1977, *Hatch 2365* (NMC). New record for New Mexico. Previously reported from Texas (Gould 1975b) and Arizona (Gould 1956).

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I thank Jose F. M. Valles, Department of Range Science, Texas A & M University, for the identification of *Urochloa* and Dr. R. F. Spellenberg, Department of Biology, New Mexico State University, for bringing the *Urochloa* and *Muhlenbergia* collections to my attention.

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STILT SANDPIPER AND HUDSONIAN GODWIT IN NEVADA

C. S. Lawson[1]

This note reports the first specimens of Stilt Sandpiper (*Micropalama himantopus*) and Hudsonian Godwit (*Limosa haemastica*) collected in Nevada. All specimens were taken at the tailing ponds in Las Vegas Wash, 24 km southeast of Las Vegas, Clark County, Nevada. One specimen of each is now in the Museum of Biology, University of Nevada, Reno, Reno, Nevada (UNMB) and one Hudsonian Godwit specimen is now in the Nevada State Museum (NSM) collection, Carson City, Nevada.

STILT SANDPIPER.— Prior to this report there were only two published records of sightings of Stilt Sandpiper in Nevada. In northern Nevada, three birds were observed 30 July 1939 in Churchill County, 24 km northwest of Fallon near Hazen by Slipp (1942, Murrelet 22: 61–62). In south-central Nevada, seven birds were observed at the Nevada Test Site in Nye County 8 October 1961 (Hayward, et. al, 1963, Brigham Young Univ. Sci. Bull. Vol. 3, No. 1: 10). I collected one bird 17 September 1976 (UNMB #1813, immature male, skull not fully ossified, gonad minute, moderate fat, weight 59.25g). Three other sight records, all from Las Vegas Wash, include the following: I observed one bird 28 April 1972 and Vince Mowbray observed two birds on two separate occasions, 16 September 1973 and 7 September 1976.

HUDSONIAN GODWIT.— There are no previous sightings of this species in Nevada. I collected two of five birds present 15 May 1976, one male and one female. The male is UNMB #1808, adult, skull fully ossified, left testes 8x3mm, light fat, weight 231.05g. The female is now NSM #1616, adult, skull fully ossified, ovary granular, largest ova 1x2mm, heavy fat, weight 279.05g. The presence of these birds had been discovered earlier in the day by Vince Mowbray.

I would like to thank Vince Mowbray for use of his previously unpublished records.

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